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## 57th ANNUAL REPORT

1903

VOL. 4

APPENDIX 8 (*continued*)

AND

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**Appendix 8** (*continued*)

## Museum memoir 7

7 Graptolites of New York. Pt 1 Graptolites of the Lower Beds

University of the State of New York

# New York State Museum

JOHN M. CLARKE State Paleontologist

## Memoir 7

# GRAPTOLITES OF NEW YORK

*Part 1*

## GRAPTOLITES OF THE LOWER BEDS

BY
RUDOLF RUEDEMANN


| | PAGE |
|---|---|
| Preface | 457 |
| Introduction | 459 |
| References | 459 |
| History of the study of graptolites | 466 |
| Methods of investigation and illustration | 479 |
| Terminology | 482 |
| Range and geographic distribution | 488 |
| Correlation table of zones faces | 490 |
| Synoptic table of distribution of species | 504 |
| Synoptic table of range of genera | 508 |
| Mode of existence | 509 |
| Mode of reproduction and ontogeny | 519 |
| Structure and morphology | 534 |
| Histology and chemical composition of the periderm | 539 |
| Classification and phylogeny of the graptolites | 543 |
| Synoptic list of fossils described | 572 |
| Taxonomic relations of the graptolites | 574 |
| Descriptions of graptolites | 578 |
| Dendroidea | 578 |
| Graptoloidea | 612 |
| Axonolipa | 612 |
| Axonophora | 718 |
| Addendum | 735 |
| Explanations of plates | 743 |
| Index | 785 |


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## PREFACE

The preparation of this memoir is the outcome of stratigraphic investigations carried on for several years in the slate belt of eastern New York. The discovery of graptolite zones affording rich and well preserved faunas new to the New York series of geologic formations, has made us acquainted with graptolite facies of the important formations represented in the time interval from the Upper Cambric to the end of the Lower Siluric. The important bearing which the distribution, correct correlation and identification of these graptolite faunas have on the geologic history of New York in earlier Paleozoic time, and on Paleozoic paleography in general, demands their monographic treatment, with special reference to range and geographic distribution.

On account of the very large amount of material to be considered, it has been deemed advisable to divide this treatise in two parts, of which this is the first. It contains the descriptions of the graptolites of the Upper Cambric and Lower Champlainic (Lower Ordovicic), leaving to the second part those of the Middle and Upper Champlainic (Trenton-Lorraine) and of the Ontaric, or Siluric.

In view of the facts that, since the publication of Hall's classical memoir on the Quebec graptolites, 40 years ago, for the Canadian Geological Survey (partly republished in the 20th annual report of the New York State Cabinet of Natural History), no statement of the general results of graptolite researches has appeared in print on this continent, and that the recent literature on this subject is widely scattered, and some of it difficult of access, this memoir is introduced by a résumé of the present status of our knowledge of graptolites.

During the prosecution of this study, I have had the constant aid and encouragement of the state paleontologist, to whom I am indebted for access to literature connected with the subject and other necessaries of investigation.

To him my most sincere thanks are due. I am also under obligation to Mr Charles Schuchert, who kindly placed at my disposal the material collected by Messrs Walcott, Dale and Prindle during the prosecution of their work in the slate belt, and deposited now in the collection of the National Museum. Prof. R. P. Whitfield has kindly allowed me access to the Quebec graptolites of the Hall collection in the American Museum of Natural History; and Mr Gilbert van Ingen of Princeton University has generously given me the benefit of his skill in photographing the obscure appendages of these organisms.

RUDOLF RUEDEMANN
*Assistant State Paleontologist*

# INTRODUCTION

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## 2 History of the study of the graptolites[1]

In examining a piece of black Siluric shale, one often notices on its surface peculiar figures which, by their form and substance suggest pencil markings. They are nearly always toothed like a saw on one or both sides. *Linné* described, together with other objects of different character, some of these markings under the very appropriate generic term "Graptolithus." This word has provided a name for the whole class of fossil organisms.

The frequently leaflike shape, serrate margin and carbonaceous substance of the fragments which alone were known to the early observers, led them to consider these bodies as of vegetable origin, a view held specially by *Bromell* and *Brongniart*, and also current among some of the members of the Geological Survey of New York, who in their works refer to the graptolites as "fucoids."

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[1] The early history of the study of graptolites has been exhaustively treated by James Hall in his memoir, *Graptolites of the Quebec Group* [§ 8, Historical notice of the genus Graptolithus, p. 59] and in his "Introduction to the study of the Graptolitidae" [N. Y. State Cab. Nat. Hist. 20th An. Rep't]. These publications well depict the progress in the conception of the graptolites from Linné onward and the state of our knowledge of this group of fossils at the beginning of the last third of the last century. Referring the reader to this earlier publication on the subject in a report from this office, we will mention only the most important events of the history up to Hall's fundamental work and restrict ourselves to a fuller treatment of the later history. The more important later investigations are also incidentally mentioned in Zittel's *History of Geology and Paleontology* [1901]; and the latest discoveries the reader will find more fully discussed in publications by C. Wiman [1895, 1896], A. Tornquist [1897], and the present writer [1898].

The first to consider the graptolites as of animal nature was *Walch*, who described two species as toothed Orthoceratites. This conception of the graptolites was subsequently maintained by *Wahlenberg*, *Schlotheim* and for a time, also by *Geinitz* and *Quenstedt*.

*Nilsson* appears to have been the first observer who pointed out the similarity of the structure of the graptolites to that of recent hydrozoans. *Beck*, *Murchison* and *Portlock* held the same view, Portlock comparing them with Sertularia and Plumularia; while *Barrande*, who first (in 1850) described exhaustively a whole graptolite fauna, that of Bohemia, disproved fully the relation of the graptolites to the cephalopods.

As early as 1847, *Hall* described and finely illustrated (*Palaeontology of New York*, v.1) one species from the Trenton and 13 species from the Utica and "Hudson river" shales of New York, stating [p. 265] his agreement with the view of Dr Beck, viz that the graptolites are to be compared with Virgularia. In 1849 he announced before the American Association for the Advancement of Science [Proc. 1849, p. 351] the occurrence of 20 species of graptolites in the Lower Siluric rocks, and of three species in the Clinton formation. The latter, together with the genus Dictyonema, have been described and figured in the second volume of the *Palaeontology of New York*.

In 1855 *Emmons* described as new 14 species, from various localities, largely from the shales of Columbia county, N. Y. and of Virginia, and three new genera, Nemagrapsus, Glossograpsus and Staurograpsus, attaching the last designation to a Cambric form, more fully noticed in the present publication.

When a finely preserved, rich and new fauna of graptolites was discovered by the Canadian geologists in the Lower Siluric rocks of Point Levis near Quebec, it was intrusted to Hall for description. In a preliminary publication [1857] 21 new species were announced from these rocks of uncertain stratigraphic position. The same fauna was more fully treated, beautifully illustrated by engravings on copper, and numerous new species from the same

rocks added in Hall's most important work on this subject, *Graptolites of the Quebec Group* [1865]. In this memoir, which is classical for the study of American graptolites, all the evidence collected up to that time by Barrande, Geinitz, Hall and other observers, is critically discussed, and the compound form of numerous Dichograptidae and the presence of a central disk, in contrast to the fragmentary material then known in Europe, fully set forth. Further, three new graptolites from the Utica shale of Lake St John, Canada, among these a compound Retiograptus, are described in a supplement.

As Hall's conception of the graptolites, laid down in this work, was adopted generally and finds on the whole, expression in the textbooks still in use, though recent investigations have greatly modified it, we here cite his most important views. He states that it is shown, both from analogies and from the mode of development or reproduction exhibited in some of the species,[1] that they are true "Polypi," and comparable to Sertularia and Plumularia. He clearly recognized the common canal as connecting the denticles ("calycles" or "cellules") of the stipes. The calycles were properly conceived as the habitations of zooids (polypi). But it was held with Barrande that all "graptolites proper" (this excludes Dictyonema etc.) had a solid axis, a view which, as we shall explain later on [p. 487], has been disproved; and that the saw-like, theciferous stipes were united by connecting processes which "were always destitute of cellules," and were therefore "funicles." Recent investigations have demonstrated the composition of these connecting processes of

[1]This refers to the discovery in the Normanskill shale in the neighborhood of Albany, of a Diplograptus with peculiar, apparently saclike appendages of the stipes, which he compared to the gonangia of the Hydrozoa. A note on this discovery had been published, together with the description of two new species from the Normanskill shale, in the 12th annual report of the New York State Cabinet [1859] and reprinted, augmented by the descriptions of five more species and several new genera from the same shales, in the *Paleontology of New York*, volume 3, supplement. As the writer has demonstrated elsewhere [1895], the siculae of Diplograptus are produced in sacs, encircling the central disk of the compound fronds, and the appendages described by Hall had probably some other function.

thecae or cellules. As to the mode of existence of the graptolites, Hall concluded that the graptolites proper "in their mature condition were free floating bodies in the Silurian seas." In regard to the genera Dendrograptus, Callograptus and Dictyonema, he held that the frequent bulblike enlargements at the base indicate attachment to bodies or an embedding in the mud. Even at the present opinions in regard to the mode of life of the graptolites are greatly at variance, and the problem has apparently not yet been solved to general satisfaction.

The introduction to the *Graptolites of the Quebec Group*, somewhat enlarged and with the addition of supplementary notes on certain genera, has been reprinted under the title, "Introduction to the Study of the Graptolitidae," in the 20th annual report of the New York State Cabinet [1868]. This publication closed Hall's work on the graptolites.

In tracing the subsequent development of our knowledge of the graptolites, it will greatly facilitate the grasp of the subject if we keep apart two different trends of investigation. As the graptolites not only became interesting and important as a class *per se*, which invited investigation by its early extinction, the great variety of forms displayed and the ignorance of their internal structure among paleontologists, but were also recognized as the most reliable and widely distributed index fossils for the determination of horizons of the Upper Cambric and Siluric, their study has been pursued from the standpoint of the biologist as well as from that of the stratigrapher.

We will first take up the investigations of the stratigraphic relations of the graptolites, as these attracted the attention of numerous geologists long before their biologic aspect. This work had naturally to begin with the descriptions of the faunas found in the rocks of various regions. It can be claimed that *Barrande* and *Hall* laid the foundations of this branch of the science by describing the graptolite faunas of Bohemia and eastern North America. At the same time, however, the exploitation of the graptolite schists of Scotland, northern England and Wales had been undertaken by the well known pioneers of British geology, among whom we enumerate

*Sedgwick*, who [1848] described graptolites from the Skiddaw slates in north England; *Salter*, who [1848] recognized some of Hall's Normanskill shale forms in the slates of Loch Ryan, described other species from the rocks of Scotland in 1851 and 1852, in 1861 proposed the new genus Dichograptus, and in 1863 Tetragraptus; *McCoy*, who erected the genus Diplograpsus [1850] and described numerous species from British paleozoic rocks, recognizing several American species among them, in the *British Palaeozoic Fossils* [1851]; and *Harkness* [1850], who described the graptolites of the black shales of Dumfriesshire, a work continued by *Carruthers* in 1858.

On the continent *Suess* [1851] added considerably to the list of forms made known by Barrande from Bohemia; and *Geinitz* [1852] described the graptolites of Saxony.

In America Hall's work found early response. *Billings* [1861] compared the zones of Europe and America and endeavored to show that the graptolite shales of Normanskill near Albany were not in the upper part of the Lower Siluric, or Hudson river group, as Hall maintained, a contention which is now decided in Billings's favor [p.490]; and *Logan* [1863] recognized the occurrence of graptolites of the Normanskill and Utica shale of New York in Canadian rocks.

The remarkable zonal distribution of the British graptolites was however not fully recognized nor understood, till *Nicholson*, *Hopkinson* and, specially, *Lapworth* began their systematic exploitation of the British graptolite shales. By their endeavors it became known that six principal divisions can be discerned in the graptolite shales of the Upper Cambric and Siluric, that these again can be subdivided into smaller subzones, and that these zones show an astonishing uniformity of succession throughout the British Isles.

When finally the same work was undertaken in Scandinavia by *Linnarsson*, it was found in Scania, where the graptolite shales are greatly developed and little disturbed, that the same principal divisions as in Great Britain could be recognized; and *Tullberg* and *Törnquist* were able to subdivide the Swedish Siluric by means of the graptolites so minutely that in all stratigraphy we find a

parallel only in the ammonite zones of the Jurassic. *Brögger* recognized [1882] a part of the zones in Norway. The presence of like associations and a similar succession have, further, been recognized by *Barrois* [1892] in Languedoc in southern France and by *Kerforne* in the Upper Siluric of Brittany [1901]. The graptolite fauna of Bohemia has, in continuation of Barrande's work, been exhaustively described by *Perner*.

Hall records [1868, p.233] that in 1861 *McCoy* sent him a proof of a plate of graptolites from the *Palaeontology of Victoria* (Australia) with illustrations of species identical with Normanskill forms. Before, however, that work appeared, *R. Etheridge jr* [1874] had made us acquainted with some of the Lower Siluric graptolites of Victoria. In decades 1, 2 and 5 of the prodromus of the *Palaeontology of Victoria* [1877–78] *McCoy* gave detailed descriptions and illustrations of these interesting graptolites from the auriferous shales of Victoria. Nearly all forms are identified with species known from the American and British graptolite rocks; and one new genus, Goniograptus, first discovered in Australia, has since been announced in the same species from the Quebec rocks by *Ami* [1889] and from the Deep kill by the present writer [1901].

In the last decade our knowledge of the faunas of the British graptolite beds has been greatly augmented by the work carried on, under the safe guidance of Lapworth, by *Elles* [1898]. These authors have now united and, with the collaboration of Miss *Wood*, have undertaken the arduous task of monographing the British graptolites and of reproducing them by the most exact illustration now obtainable. Two instalments of this monumental work have already appeared.

At the same time the stratigraphy of the English graptolite rocks has been much furthered by the investigations of *Marr* [1889, 1894], who has also extended his labors to the graptolite shales of Thuringia and the Fichtelgebirge in Germany, the former field of *Richter's* discoveries, while for the Welsh Upper Siluric a zonal mapping based upon graptolite zones has been carried out by *Elles* [1900], *Wood* [1900] and *H. Lapworth* [1900].

In America the work on the graptolites has rested for a long time, partly on account of the unpromising character of the graptolitiferous rocks and partly because the many new fields of investigation offered by a large continent, completely held the attention of the small band of paleontologists. *Lapworth* [1886], however, demonstrated the general parallelism of the succession of the faunas of Canada and Great Britain; *Matthew* [1891, 1895] brought out some important facts incidental to his investigations in the St John basin; and *Ami* [1888] has published lists of graptolites from numerous outcrops of the Lower Siluric in Canada. *Spencer* [1884] described a number of graptolites from the Upper Siluric of Canada and the West. A systematic exploitation of the graptolites of North America was commenced by *Gurley* [1896], but unfortunately the work has not been continued. *Ruedemann* has published observations on graptolites of the Utica shale [1895] and in later years undertaken the investigation of the "Hudson river shales" of New York, demonstrating their composition of a series of graptolite zones, ranging from the Upper Cambric to the Upper Champlainic [1901, 1902, 1903].

The elucidation of the morphology of the graptolites, of their internal characters, of the structure of the proximal portions and of the mode of development has met an almost prohibitive obstacle in the flattened condition of the shale material; and only the untiring patience of some observers and a few fortunate discoveries of superior material have from time to time brought forth essential facts.

As, in the discussion of the morphologic characters of the graptolites, we shall have occasion to recur in greater detail to the views of preceding observers, it suffices here to mention only the most important advances made in this branch of graptolitology.

The first resolutely to attack the problem of the internal structure of the graptolites was *Barrande*. He first asserted the invariable presence of a solid axis or "virgula" in graptolites, introduced the term "common canal" for the tube connecting the cells and claimed that forms with a double row of cells have also a double common canal. Barrande also held that the

extremity of the stipes with the smaller cells, was the younger one, and recognized two subdivisions, namely Monoprion, with a single row of cells, and Diprion, with a double row. As we shall see later on, nearly all of these opinions of the pioneer have been greatly modified. Indeed, only a year after the publication of Barrande's work, *Scharenberg* [1851] in Norway, corrected some of Barrande's conclusions, without however finding direct followers. He claimed that the division into Monoprion and Diprion excludes the branching forms, that in Diprion there are not two independent series of cells, but the latter alternate without exception, and he also asserted that the narrower extremity is not necessarily the younger.

*Hall* adopted Barrande's views as to the presence of a solid axis in all forms and as to that of one or two common canals, in Monoprion and Diprion respectively. He retained however all forms in the genus Graptolithus, on account of the discovery of forms, as G. r a m o s u s, which show "the occurrence of both a single and a double series of cellules upon the same stipe" [*loc. cit.* p. 40]. He also considered the use of the terms Tetragraptus and Dichograptus impractible, as for the most part only fragments of stipes are found, which would not allow these distinctions. At the same time his material was the first to exhibit the multiplicity and complexity of forms of branching graptolites, which soon led to such an extended subdivision of these branching forms that it is now claimed [*see* Frech] to have gone beyond the proper limits.

*Hall* also made important additions to our knowledge of the central or basal portions of the colonies. These were the recognition of an initial process in many forms, which he termed the "radicle" or "initial point" and considered the beginning of the solid axis. It is now, under the term "sicula" introduced by *Lapworth*, known as the mother theca of the colonies. *Scharenberg* and *Richter* had also pointed out the presence of this organ, the latter calling it the "Fuss."

*Hall* further concluded that there is in the branching forms a central connecting process, which he thought to be always destitute of cellules and for which he introduced the term "funicle." The opinion concerning the presence

of such a funicle has also changed in the last years. And finally he showed in several forms the presence of a disklike expansion of the proximal portion, for which he introduced the term "central disk."

In the succeeding years discussions of several genera appeared, viz of Didymograptus and Climacograptus by *Nicholson* [1867, 1870], and of Dicranograptus, Dicellograptus and Diplograptus by *Hopkinson* [1870, 1871].

The year 1872 brought the valuable publications of *Allman*, namely his *Monograph of the Gymnoblastic Hydroids*, which contains a chapter on the graptolites, and his treatise *On the Morphology and Affinities of the Graptolites.* We shall have occasion to notice his views in greater detail in succeeding chapters, and, therefore, mention here but the most important inferences. Allman holds that the presence of the virgula, or "solid axis," the fact which most obviously opposes itself to an acceptance of the hydroid affinities of the graptolites, though an extremely exceptional structure, can hardly be regarded as offering an insurmountable obstacle to the admission of the graptolites into immediate relation with the Hydroidea, in consideration of a solitary genus, Rhabdopleura, with a similar rod among the bryozoans. The calycles of the graptolite, he compares, on account of their uninterrupted internal passage into the common canal, with the nematophores of the Plumularidae, and the supposed capsulelike bodies, described by *Nicholson* and *Hopkinson* as gonangia or gonophores, he believes to have had but accidental connection with the graptolites. He is inclined to consider the graptolites "a very aberrant hydrozoal group having manifest affinities with the Hydrozoa."

While the exploitation of new graptolite fields in southern Scotland [*Hopkinson* 1872, *Lapworth* 1872], in Shropshire [*Hopkinson* 1873], in the Hartz [*Lossen* 1874] was taken up with energy, *Lapworth* began the systematic work on the distribution and classification of the British graptolites, which has furnished the basis for our present correlations of the graptolite horizons and for the systematic arrangement of the multitude of forms. In his paper, "On an Improved Classification of the Rhabdophora," he pointed out the development of the colonies from a "germ," called by him the "sicula,"

for which hitherto indefinite terms as "radicle," "radicular bar" and "axillary spine" had been used. He also recognized the formation of a solid axis in its wall, a fact verified later on by *Wiman*, emphasized its importance for specific distinction and defined the "angle of divergence," and arranged the genera into families, which were brought under the subdivisions erected before by *Hopkinson*. This system will be further noticed in a later chapter [p.544].

*Herrmann* [1885] monographed the family Dichograptidae and *Jaekel* [1889] published observations on graptolites obtained from diluvial boulders, demonstrating the presence of an important difference in the thecal structure of the species of Monograptus.

While the faunas of various regions had been thoroughly described and a great number and variety of forms made known; the succession of the faunas and faunules had been established and an elaborate system of zones obtained in several countries and these zones had been parallelized, thus demonstrating a wonderful rapidity in the development of the graptolite genera and their distribution over vast areas, still the problems of the internal structure remained as unsolved as they had been left by Barrande and Hall. This can not be wondered at, as the flattened carbonized specimens which constitute nearly all collections are unfit for an elucidation of the internal characters.

It is true that a few keen observers drew some correct conclusions from such material; but, as these were not readily verified, they did not find general acceptance. Thus it was claimed by *Scharenberg* that the Diprionidae are in fact Monoprionidae, produced by an alternate gemmation of thecae; and *Lapworth* expressed his belief, when describing two species of Dimorphograptus [1876], that there are no diprionidian forms, and the sicula in all graptolites produces but one bud. These views of Scharenberg and Lapworth, gleaned from shale material, have been found to be correct by recent investigations on specimens etched out of limestone. Positive evidence was however not obtained till the preparation of sections of graptolites was begun.

*Törnquist* [1881, 1892] first undertook the study of sections through pyritized specimens, mostly diprionid forms, and observed the connection of virgula and sicula, the position of the sicula on one side of the rhabdosome, the presence of a "connecting canal," which connects the sicula and the thecae, and the position of the virgula or solid axis within a median septum, but his material did not furnish him any positive evidence in regard to the single or double character of the common canal of the diprionid forms.

A better insight into the structure of the graptolites was obtained by the methods of dissolving graptolitiferous limestone, first applied by *Gümbel* [1878], then used successfully by *Holm* and finally brought to considerable perfection by *Wiman*.[1]

Holm elucidated, by means of such material, the structure of Retiolites and Stomatograptus [1890], among the diprionid forms, and of Didymograptus, Tetragraptus and Phyllograptus [1895] among the Dichograptidae. He demonstrated the composition of the "funicle" of thecae in the first two named Dichograptidae, the perfect conformity in the development of the proximal parts in all three genera and the fact that the frond of Phyllograptus is composed of four stipes, coalesced at their dorsal sides. [For further details of his results *see* the generic and specific descriptions of Phyllograptus, and ch.10]. The same distinguished author also first observed the presence of smaller tubes attached laterally to the thecae in a species of Dictyonema, thus giving the first intimation of the complex structure of the dictyonemas.

*Wiman* [1893, 1895] demonstrated by his refined methods the bilaterally symmetric form of the sicula and its composition of two parts, the initial part of which is continued into a hollow rod, the nema; he also showed the initial distal growth of the first theca and its later reversion, and the origin of the double row of thecae of Diplograptus and Climacograptus from one theca, thus verifying Scharenberg's and Lapworth's assertion, that the so called diprionid forms are also monoprionid. His important results on this subject will be noticed more in detail hereafter. By the application of the microtome

[1] See description of these methods in ch. 3, p. 480.

to the Dendroidea, which were hitherto, as regards their internal structure, practically untouched, he demonstrated the complex character of the rhabdosomes of Dictyonema, Dendrograptus and Inocaulis, proving that they are composed of three kinds of theca.

The **histology** of the periderm first received attention from *Richter* [1871], and later from *Gümbel* [1878]. No very elaborate investigations of the test were made, however, till *Perner* [1894] undertook the study of the Bohemian graptolites. His results have been modified quite essentially by *Wiman's* [1895] and *Gürich's* [1896] work. [For further details in regard to the histology of the periderm *see* ch. 9, p. 539]

The **mode of reproduction and development of the graptolites** is a field still very little exploited. For investigations of this nature, a large collection of growth stages of one species in the best state of preservation is prerequisite, a condition rarely fulfilled. *Hall* has figured [Can. Grapt. pl. B] some "germs" without referring them, however, to a special type. In his "Notes upon the Genus Graptolithus" he figured stipes of Diplograptus whitfieldi, bearing saclike appendages, which he regarded as reproductive organs. *Nicholson* [1867] observed numerous variously shaped corneous bodies in the graptolitic shales, which he thought to be remains of capsules, termed "Dawsonia" and held to have been "ovarian vesicles" or "gonophores" of graptolites. As we shall see presently [p. 738 and under Dawsonia, p. 521], most probably neither of these bodies has anything to do with the multiplication and propagation of the graptolites. In fact, *Nicholson's* assertions were very soon objected to by *Carruthers* [1868], who insisted that these bodies had no resemblance to the "gonophores" of the Hydrozoa, with which Nicholson had compared them. The same author proposed also to transfer the terminology introduced by *Allman* and *Huxley* for the Hydrozoa to the graptolites [for further details *see* p. 482] and furnished a detailed analysis of the relations of the graptolites to recent similar organisms; whereby, by a process of exclusion, he concluded that they are most nearly comparable to the Sertularians, but differ principally in the

presence of the solid axis which at that time was still supposed to be present in all graptolites proper.

The investigation of the proximal parts of the rhabdosomes of Tetragraptus and Didymograptus by *Holm*, and that of the stipes of Diplograptus and Monograptus by *Wiman*, allow a conclusion as to the mode of development of these portions of the colonies. The latter investigator succeeded also in elucidating the mode of reproduction of thecae in Dictyonema, Dendrograptus and Inocaulis.

*Ruedemann* [1895] obtained a complete growth series of Diplograptus foliaceus and was, with the aid of this material, able to trace the development of the whole colony of that species from the sicula onward [p.528]. Later, a like series has been secured for a multiramous dichograptid, viz Goniograptus thureaui [p.622 and pl.6]; and in this memoir the development of Dictyonema flabelliforme is described [p.602 and pl.1].

The study of the **phylogeny** of the graptolites, aside from the attempts at mere classification by various authors, was not taken up till the last decade. *Wiman* derived different groups of Monograptus, each by way of its corresponding Dimorphograptus, from Diplograptus and Climacograptus, thus indicating the polyphyletic origin of that genus; and *Nicholson* and *Marr* [1895] have outlined the path of development of the Dichograptidae, taking the shape and arrangement of the thecae as characters of prime phylogenetic importance. Their results point also to a polyphyletic origin of the large genera of this family and specially of Tetragraptus and Didymograptus. Their work has been largely verified and ably continued by *Elles* [1898].

The **mode of existence** of the graptolites, finally, has as a rule been touched only incidentally, but the problem has lately been discussed by *Lapworth* [see *Walther* 1897].

### 3 Methods of investigation and illustration

There is hardly any other group of fossils which is so uniformly bound to a definite kind of rock as the graptolites are to argillaceous shale and slate. Graptolites and graptolite shales are terms which are closely associated in the minds of geologists. As the shale yields more readily to orogenic forces than any other rock and therefore, besides being thinly bedded, is nearly always pressed into small folds and thoroughly cleaved, a shale terrane may be filled with graptolites and yet furnish but little material that is fit for an investigation of these delicate bodies. This unfortunate state of preservation is well known to collectors and also strongly prevalent in the graptolitiferous shale region of New York, the greater part of which, namely, the entire territory bordering on and east of the Hudson lies within the region which has been subject to the Appalachian folding. Hence, while there are graptolite localities of most zones in large number, very few furnish satisfactory material.

In this slate or shale the specimens are as a rule flattened to such a degree that but very faint relief is shown, and the graptolite has become nothing but a tenuous film. The keenest and best trained observers, as Barrande, Hall and Lapworth, notwithstanding untiring efforts, have therefore, been unable to arrive at a correct conception of the structure of the stipes of some of the most common forms, such as Diplograptus, from the study of shale material.

But, as if to atone for this failure to furnish structural details, the shale preserves the outlines and general form of the multiplicity of types distinctly and in very accessible state, sometimes even retaining the entire compound colonies neatly spread out on the bedding planes; and often there are stored in it myriads of various growth stages, which are so well preserved that one is at times able to retrace the entire ontogenic development of a type, as the writer has done in the cases of Diplograptus foliaceus, Goniograptus thureaui and Dictyonema flabelliforme.

Another advantage of the shale material, of equal importance to the stratigrapher and the student of the phylogeny of the graptolites, is the fact that the graptolite shales, being slow deposits, frequently contain rapidly changing graptolite faunas within a very limited thickness of rock, as in the Deep kill section which has furnished the principal material for this memoir.

As stated before, the flattened shale material allows the elucidation of but very meager facts bearing on the internal structure of the graptolites. Sometimes, however, these bodies became centers of crystallization, mostly of pyrite, and have thus been protected from flattening and crushing forces. Such pyritized specimens have been used for the preparation of sections by *Törnquist* [see p.476]. A layer of graptolite bed 2 in the Deep kill section contains numerous pyrite nodules, mostly with specimens of Phyllograptus ilicifolius; and the writer has been able to obtain from thin sections of these, certain facts as to the structure of the stipes and of their periderm.

The best results, however, have been acquired by the study of the graptolites which are sometimes found embedded in limestone, calcareous shale or chert. By means of sections uncompressed specimens which were preserved in more or less calcareous beds, have been studied by Perner (Monograptus and Retiolites), Gürich (also Monograptus) and by Holm (Phyllograptus).

In calcareous or flinty beds the graptolites can be further etched out with acids without crumbling to pieces, as those of argillaceous shale will do under such treatment. This method was first applied by Gümbel [1878], but has been brought to great perfection by Holm and specially by Wiman.[1]

Limestone material was found the simplest to handle, and muriatic acid in different states of solution or milder solvents such as acetic acid, gave good

[1] Dr Wiman has published an interesting account of his preparative methods in his paper "Über die Graptoliten" [1895] and in the "Structure of the Graptolites" [1896]. His work has been reviewed in the *American Geologist* [1896] by Clarke, and in the *American Naturalist* [1898] by Ruedemann.

results in dissolving the matrix. Strongly argillaceous marl slates were first treated with acetic acid, which dissolves the lime content, and then the graptolites were brought out with hydrofluoric acid. In silicious rocks, mostly chert masses, graptolites have been freed with concentrated hydrofluoric acid.

The isolated graptolites have been decolored by Holm and Wiman in different ways. Wiman used first Schultze's maceration medium, which is a solution of calcium chlorate in nitric acid, but later substituted for it eau de Javelle or potassium hypochlorite, because Schultze's medium is often too harsh. The specimens were then cleared with chloroform or other clearing fluids and mounted in Canada balsam. Where this method could not be used on account of the thickness of the periderm, they were prepared for the microtome according to the methods used by zoologists.

The **methods of illustration** of graptolites have also been gradually improved. Minute isolated specimens and thin sections have been drawn with the camera lucida by Holm and Wiman and thus accurate representations obtained. As the specific distinctions of the graptolites have frequently to be sought in minute details, such as the inclination and closeness of arrangement of thecae, the former method of free-hand drawing with its unavoidable idealization of the figures, is no longer sufficient to bring out the crucial characters with the desired accuracy. Fortunately the shale material as a rule retains just enough relief to permit its being drawn with the camera lucida or even being photographed as Barrois has done. Van Ingen has also successfully photographed graptolites of the St John group and then used the photograph for tracing [Matthew 1895]. By his kind assistance I have been enabled to bring out characters photographically which were visible to but few observers.

Lapworth has had constructed, for the illustration of the British graptolites in the monograph now under preparation, a horizontal microscope with attached camera lucida. By means of this arrangement the specimens can be enlarged with the least possible slanting to five times natural size. The drawings have then been shaded and reduced by photographic

process. The collotype plates thus obtained, miss, it is true, the artistic effect that so distinguishes the former illustrations of graptolites and specially the beautiful engravings in Hall's *Graptolites of the Quebec Group*, but they are clearly faithful representations of the specimens in natural size.

As our facilities did not permit us the application of Lapworth's method, which would appear to furnish the most satisfactory results, we have drawn the outlines of all forms, which are enlarged by means of a vertically placed compound lens with attached camera lucida, the light being furnished by a Bausch illuminating lens. This arrangement necessitated very little slanting of the slabs, and the slight distortion produced by the inclined position of the slabs has been reduced to a minimum by the placing of the longitudinal axis of the fossil in a diagonal position. These outlines have been reduced by photography to a scale of mostly twice natural size, this small enlargement being retained to secure more distinct representation of certain details than the natural size drawings could furnish. The text drawings are slightly reduced camera drawings. The illustrations in natural size have been traced with a lithographer's needle directly from the fossils on gelatin plates, glued over the graptolites. After retracing on the other side of the gelatin plate, the outlines have been transferred to paper by means of lampblack, rubbed into the tracings. While this method can not give exact results with minute objects and hence is subject to various sources of error, it not only gives satisfactory results with larger fossils, but also saves much time and labor.

### 4 Terminology

The terminology which is currently applied to the graptolite structure has been transferred to this extinct class from the hydrozoans under the assumption that the graptolites form a branch of the Cnidarians. This usage can be objected to on the ground that the taxonomic relations of the graptolites are not yet established. It seems however that, inasmuch as a terminology is necessary, and the graptolites indeed in their structure show more analogies and similarities to the Hydrozoa than to any other class of living animals, a leaning toward the hydrozoan terminology appears most

practicable, while the presence of distinctive features makes the creation of certain new terms imperative.

As numerous terms have been applied to almost every part of the graptolite structure, it is advisable to define the terms here used before entering on a description of the forms and a discussion of their structure.

The term *hydrosome* means "the whole colony" in the terminology of the hydrozoans. For the whole colony of the graptolites the terms *frond*, *polypary*, *polypidom*, *polypier*, *polypariet*, *colonie* and *Stock* also have been used. Törnquist has proposed to use for hydrosome the more neutral term *rhabdosome*, which has been adopted by Wiman. The rhabdosome of a graptolite could be defined as each colony which originates from a sicula. Here arises, however, a difficulty from the fact — discussed fully in the chapters on embryology and morphology of the graptolites — that, while in the Dendroidea and Dichograptidae each colony originates from one sicula, in the later forms, the Axonophora (Diplograptus etc.) generations of secondary colonies, produced by the primary colony, and each of which also originates from a sicula, remain in connection with the mother colony and thus form a compound colony or a person of a still higher order (the bushlike stocks of Diplograptus etc.). These are hence colonies of colonies, or a combination of rhabdosomes. It would probably be advantageous to apply to these combination colonies a term like *synrhabdosome*, expressive of their composite character.[1] As formerly the "stipes" (rhabdosomes) of Diplograptus, Climacograptus and other later genera were considered as representing the whole colony, the terms hydrosome, rhabdosome, polypariet etc. have been applied to these as well as to the entire colonies of the Dichograptidae and Dendroidea. This usage happens to be correct in consequence of the homology of both now recognized.

[1] The writer has in a previous paper on Diplograptus [1895, p. 224] termed the compound colonies of Diplograptus hydrosomes and the component colonies rhabdosomes, a usage which, however, does not appear to express the homology existing between the components of the Diplograptus colony and the whole colony of the Dichograptidae.

Frech proposes to reject both terms, hydrosome and rhabdosome, hitherto in use for these stipes, as indicating that the latter embrace the whole organism, and to use instead the term *hydrorhabd.* This term, again, is open to the objection that it suggests the hydrozoan nature of the graptolites. The term polypary, still in common use (also in *Monograph of the British Graptolites*) implies the close taxonomic relation of the graptolites to the Cnidaria. We shall for this reason here use the term *rhabdosome* for the colony originating from a sicula and *synrhabdosome* for the compound colony of the later forms. The rhabdosomes are persons of the second order, being composed of thecae (or persons of the first order), and the synrhabdosomes are persons of the third order, being composed of those of the second order.

The single hollow cone, from which the rhabdosome proceeds, was originally termed the *radicle* or *initial point* (*ex parte*), *Fuss* and *Haftorgan.* Lapworth has introduced the term *sicula* for it. Holm termed it the *first theca.*

Törnquist and Wiman have applied the term *connecting canal* to that part of the first theca which connects the sicula with the common cavity of the rhabdosome. Holm calls the proximal part of the second theca, which crosses the sicula, the connecting canal. Elles and Wood call this part the *crossing canal.*

That aspect of the rhabdosome, in which the sicula is visible in its entire length, is termed the *obverse aspect* (*Siculaseite*), the other, in which it is more or less covered by the connecting canal, the *reverse aspect* (*Antisiculaseite*). That end of the rhabdosome which contains the sicula is most practically termed the *sicular* end, instead of proximal end, and the other the *antisicular* end.

The rhabdosome of most graptolites divides into branches. These branches are known as *branches, stipes, Arme, Zweige* and *Grenarne.* We call here forms with many branches *multiramous*, forms with few, *pauciramous.* Forms in which the thecae are arranged in one series were called by Barrande and later writers *monoprionidian*; those in which they are arranged in two, *diprionidian.*

There has prevailed much difference of opinion in regard to the proper

conception of the *angle of divergence* of the branches. The fact of the gradual reversion of the branches from a descending to an ascending position is readily expressed by the use of Hopkinson's definition of the angle of divergence as the "angle included within the polypiferous margins of the branches."

The variation of the angle of divergence and of the curves described by the branches, has made it expedient to introduce terms for a number of characteristic positions of the branches, which will save long descriptions. These are *dependent*, *declined*, *deflexed*, *horizontal*, *reflexed*, *reclined* and *recumbent branches*. The terms find their explanation in the appended diagram.

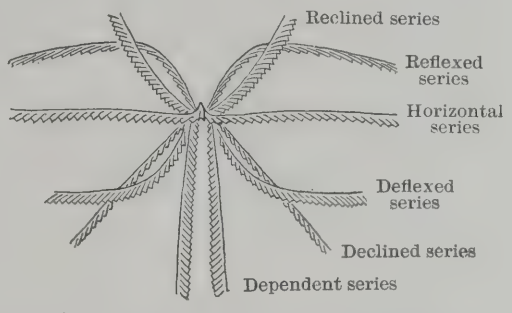



Fig. 1 Diagrammatic figure, showing the relative angles of divergence of the branches characteristic of the several series of Didymograpti [Copied from Lapworth, Elles & Wood]

A difference has been noted between *dichotomous* and *monopodial* [Wiman] or *lateral* [Elles] branching. In the first both diverging mother thecae of the new branches assume directions different from that of the older branch, while in the monopodial branching only one mother theca of a new branch turns aside. Where repeated divisions produce numerous generations of branches, the self-explaining terms, *branches of the first, second,* etc. *order,* are used to denominate the successive generations.

The receptacles of the zooids passed originally under the designations, *denticles*, *calycles*, *cellules*, *cells*, *cups* and *Zähne*, and were later on called *hydrothecae* like the analogous parts of the hydrozoans. At present the term *thecae*, (*Theken*, *Thekorna*) has found nearly universal usage. Lapworth has lately used the term *graptothecae* [1897, p.251]. Frequently the zooids, which once inhabited the thecae, are meant by the expression thecae, a usage which, though illogical, can, as Holm has pointed out, hardly be avoided, if long paraphrases are not to be used. As a matter of fact, the shells are in paleontologic literature currently treated as the individuals. The thecae represent the *persons of the first order.*

The distal end of the theca is the *aperture.* In describing the thecae, one regards them as bounded by four walls, viz one *dorsal* (inner), one *ventral* (outer), and two *lateral walls.* The distal free margins of these walls constitute collectively the apertural margin. The ventral region of the apertural margin forms a well marked denticle and is sometimes prolonged into an *apertural spine.* The *length of the thecae* is conventionally measured by the ventral margin. The latter is in contact with the dorsal wall of the theca immediately preceding it, or overlapped by it to a certain fraction of the length of the thecae.

The walls of the rhabdosomes, which in the living state were chitinous, are cited as the *periderm, perisarc, test, Haut* and *Schale.*

The proximal parts of the thecae form a canal in the Graptoloidea. This is termed the *common canal, coenosarcal canal, gemeinsamer Canal, canal commun.* The outer edge of this common canal is termed the *dorsal edge.* A view of the compressed stipes, in which only this canal is exhibited, is a *dorsal view.* The opposite margin, which is denticulated by the outer margins of the thecae, is the *ventral margin,* and the corresponding view is the *ventral* or *frontal view* (scalariform aspect). In the *profile view* both the dorsal and ventral edges are seen.

Hall proposed the term *funicle* for the central connecting process and its subdivisions in the Dichograptidae, which he thought to be destitute of thecae. Since, however, these central parts have later on turned out to be also composed of thecae, the term is no longer applicable to them. The writer [1895, p.222] had applied Hall's term to the small, long elliptic chitinous vesicle from which the nemacauluses of Diplograptus spring. Wiman [1895, p.73] has pointed out that this so called funicle of Diplograptus is a different part of the graptolite colony from that which Hall termed funicle in the Dichograptidae; he concedes however that it may be identical with the part of Retiograptus called funicle by Hall. As, indeed, the composition of the synrhabdosomes of Retiograptus and Diplograptus is identical, both representing persons of the third order, and the central parts, termed here funicle, are stems which are destitute of thecae, the term no longer necessary for the Dichograptidae could

be properly transferred to them. The funicle is, then, the common base of the nemacauluses of the rhabdosomes or persons of the second order in the Axonophora, or one of the central parts of the person of the third order, while the "funicle" of the Dichograptidae represented but the central part of a person of the second order.

The sicula is suspended by means of a flexuous, filiform process which has been termed the *nema* or *linea* by Lapworth [1897, p.251], and *hydrocaulus* by the writer [1895, p.224]. In the last cited paper it has been shown that the proximal prolongation of the axis of the rhabdosome of Diplograptus known as *virgula* is identical with this nema or hydrocaulus. This latter is a hollow process, capable of further growth. There originates however in the wall of the sicula of the Axonophora, as Wiman has demonstrated, a solid rod, to which the latter author has applied the name *virgula*. This rod is not present in the sicula of the Axonolipa, and, as the writer's observation would indicate [1897, pl.2, fig.6], it extends into the nema of the Axonophora.

A sharp distinction between the hollow proximal prolongation of the sicula, present in all Graptoloidea, and the solid axis, originating in the wall of the sicula of the Axonophora and probably extending into the first named prolongation, hence becomes necessary. For this reason, the writer had proposed to name the hollow process hydrocaulus and the solid axis the virgula. As the term hydrocaulus is however taken from the Hydroidea, where it represents an analogous process, connecting the first receptacle of the embryo and the disk of attachment [*see* ch.7, p.523], it appears practical to discard it for one of the neutral terms, *nema* or *nemacaulus*, proposed by Lapworth. The term nema would well express the flexuous character of this organ in the Axonolipa, and the term nemacaulus the more rigid character in the Axonophora.

In certain Dichograptidae the bases of the stipes are "united by a thickened corneous expansion" which was termed by Hall the *central disk*. The writer has observed a chitinous disk in the early stages of various forms [*see* ch.7, p.535], from which the sicula is suspended. This we call here the *primary disk*, as it is clearly a more or less essential part of the first growth

stage coming under notice. The disk forming the center of the synrhabdosome of Diplograptus is a further development of this primary disk and should, hence, not have been termed a "central disk," as was done on a former occasion by the writer.

*Basal cyst* or *pneumatocyst* has been applied to a tenuous chitinous vesicle, observed in Diplograptus by the writer, which is supposed to have served as a "float."

*Dendroidea* Nicholson. This term embraces the dendroid graptolites.

*Graptoloidea* Lapworth. These are the graptolites proper.

*Retioloidea* Lapworth. In this group the periderm consists of a network of chitinous filaments.

*Axonolipa* Frech. In this order the virgula or solid axis is lacking.

*Axonophora* Frech. The forms of this order are provided with a virgula.

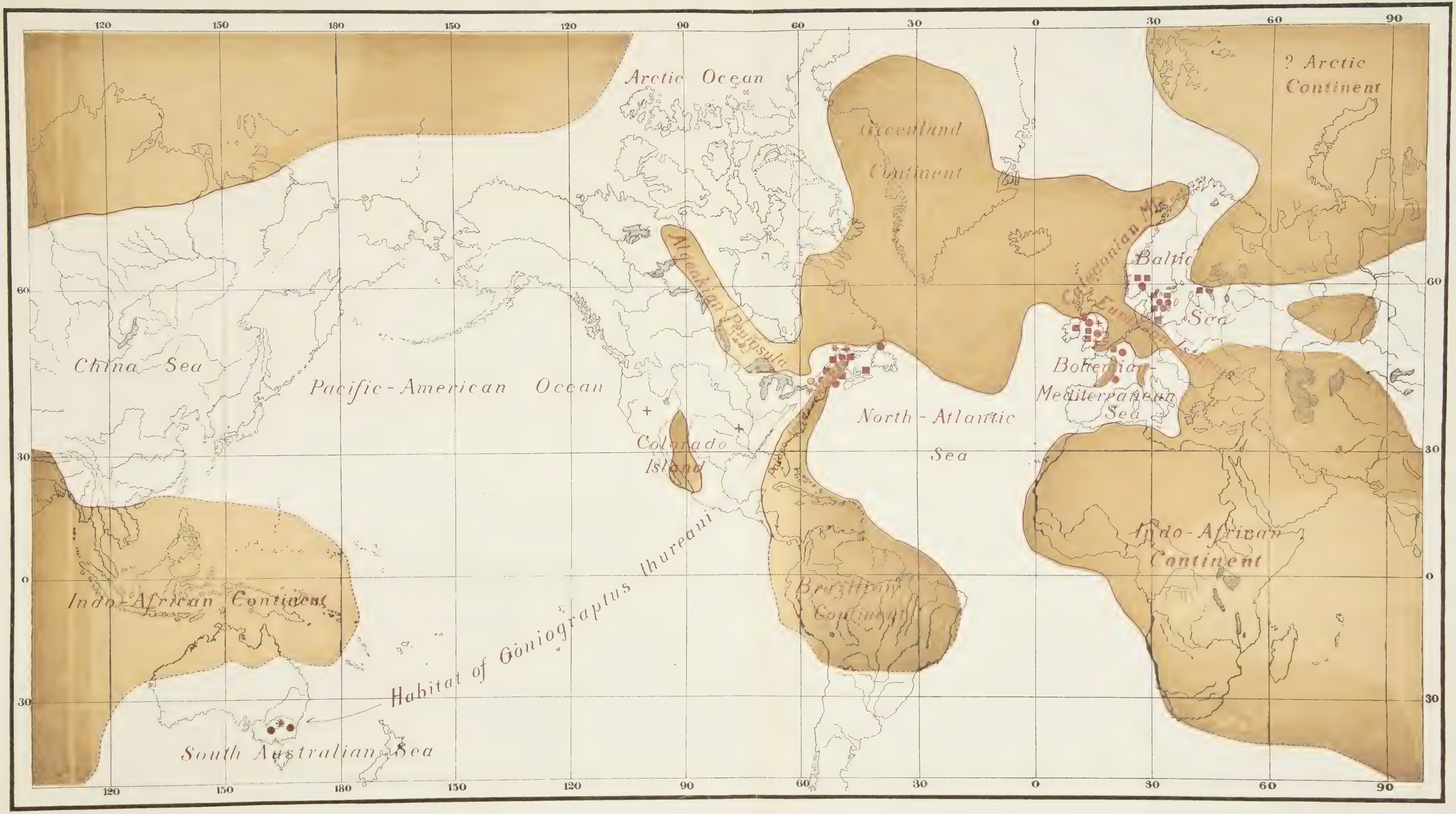
### 5 Range and geographic distribution

The graptolites begin with a few undoubted forms in the closing stage of the Cambric, attain their acme in the Champlainic (Lower Siluric), reach a second, minor period of prosperity with a small group of newly developed genera in the lower and middle Siluric and disappear with astonishing rapidity in the Upper Siluric, leaving but a few stragglers (four species in North America) in the Devonic.[1] For this reason they can be considered a class of organisms most characteristic of the Champlainic and Siluric eras.

During the period of their greatest vitality they attained a remarkable rapidity of development, which has permitted the division of the graptolite shales of several regions into a great number of life zones. This is notably the case in certain parts of Sweden, where, for instance, Tullberg cites from Scania [1882] no less than 26 graptolite zones of the Lower and Upper Siluric. This fact, together with the discovery brought out by investigations in Great Britain, France, America and Australia, that the larger divisions

[1] Gurley has also described a fossil from the Choteau limestone (Carboniferous) of Sedalia Mo. as Dictyonema blairi. This, however, is very doubtful and according to last accounts only the remains of a plant.

Chart of the World showing the Distribution of the Lower Graptolite Faunas




Legend

Land areas at the beginning of the Champlain (Lower Siluric) era in drab tint; their boundaries copied, with some alterations, from Frech [1897]

■ Localities of zone with Dictyonema flabelliforme

● " " Tetragraptus-Phyllograptus zones (zones 1 and 2 of Deep kill section)

⊦ " " zone with Diplograptus dentatus (zone 3 of Deep kill section)

* " " Goniograptus thureaui

can be recognized over immense areas, has given to the graptolites their well known reputation as reliable indicators of homotaxial beds. It is the merit of Linnarsson, Törnquist and Tullberg in Sweden, and of Lapworth in Great Britain to have brought into general recognition the fact of the possible correlation of the graptolite beds in different regions, and of their subjection to the general law of progress and development of the organic world, and thus to have freed them from the bane of suspicion which the theory of colonies, promulgated by Barrande, had brought on all correlation by graptolites.

The elaboration of the European graptolite faunas has shown that the graptolites, in their development, have three times in succession changed their plan of structure and thus produced three large divisions, by which also the zones can be divided into three large stratigraphic divisions. These are that of the deeper Lower Siluric, which is characterized by the Dichograptidae, or uniserial forms without axis; the higher Lower Siluric, in which the biserial forms with axes, the Climacograptidae and Diplograptidae, impress their character on the faunas; and that of the Upper Siluric, in which the Monograptidae, the uniserial forms with axes, hold the field almost to the exclusion of all other forms.

Of these the two first divisions are well represented in the graptolite fauna of New York. The faunas of the first are the subject of the present memoir, while those of the second division, which find their typical representation in the Normanskill fauna, will be treated in a succeeding publication. The third division, so richly developed in many parts of Europe, as Sweden, Great Britain, Bohemia and France, is hardly more than suggested by a few species found in the Clinton shales.

To the correlation of the North American graptolite horizons with the European zones on one hand and with the standard formations of this State on the other, but little attention has thus far been paid. The difficulties here are of the same character as those with which Nicholson, Lapworth, Marr and others have had to contend in Great Britain, namely an indescribable confusion of the beds by extensive orogenic movements of this part of the earth crust.

For English as well as American geologists, therefore, the Swedish beds, which are found in undisturbed or slightly altered position, must remain the standards of succession.

The identity of a considerable number of forms from the Arenig beds of the Lake district in north England and of Wales with species described by Hall from the Quebec beds, and of English Llandeilo graptolites with those of the Normanskill fauna, was early recognized, and these American terranes, accordingly, roughly correlated with English formations.

Regarding the succession of the minor divisions of the known graptolite terranes of eastern North America there prevailed, however, in consequence of their disturbed position, certain wrong conceptions; and these, having received Hall's authoritative confirmation, enjoyed for a long time an unhesitating acceptance. One of these was the placing of the "Hudson river shales" as a mass with their Normanskill and other faunas in the uppermost Lower Siluric, above the Utica shales.

When Lapworth [1886] was given an opportunity to study a collection from various localities in Canada, he recognized in them the Cambric Dictyonema zone, the Phyllograptus anna zone, the Normanskill zone and the Utica zone, and by reference to the succession of the zones in Europe he asserted that the Phyllograptus zone must correspond to a part of the lowest Lower Siluric, and the Normanskill zone should be placed provisionally between the Chazy and Trenton, at any rate below the Utica. Ami [1890] inclined to a similar correlation of the Normanskill shale on account of its association with rocks of apparently Lower Trenton aspect in the Quebec fault block; and Gurley, after an investigation of the North American graptolites, concluded that "the vertical succession of the American graptolites represents a complete parallel to the range in other countries."

The present writer has shown [1901] that in the so called "Hudson river shales" of the neighborhood of Albany there can be discerned a number of faunal zones, running parallel to the strike of the beds, from which the succession, in ascending order, of the Normanskill fauna, the Utica and Lorraine faunas with several transitional faunules can be established [*see*

| Formation | Slate belt of New York | |
|---|---|---|
| Lorraine | Zone with Dipl. foliaceus, Coryn. curtus and Lorraine fossils (Waterford) | Lorr |
| Utica | Zone with Dipl. quadrimucronatus, D. foliaceus, D. pusillus, Coryn. curtus, Triarthrus becki etc. (Rural cemetery, etc.) | Utic q (Q to St |
| | Transitional zone with Climacogr. caudatus, Cryptogr. tricornis, Triarthrus becki etc. (Mechanicville, Van Schaick island) | |
| Trenton | ? Upper Dicellogr. zone (Lansingburg power-house) | Upp an (= n |
| | Zone with Dipl. amplexicaulis (Troy) | |
| | Lower Dicellogr. zone (Normanskill beds) | Low et C La Beds |
| Chazy | Zone with Dipl. dentatus and Cryptogr. antennarius (Deep kill) | Poir |
| | Transitional subzone (Mt Moreno) | |
| Beekmantown | Zone with Didymogr. bifidus and Phyllogr. anna (Deep kill) | St ar sh D |
| | Zone with Tetr. (Deep kill) | Mai (( |
| | subz. *b* Goniogr. subzone | |
| | " *a* Clonogr. subzone | |
| Top of Upper Cambric | Zone with Dictyonema flabelliforme (Schaghticoke etc.) | Dic zo St |
| Middle Cambric | No graptolites | No |

CORRELATION TABLE OF THE ZONES IN THE CAMBRIC AND CHAMPLAINIC (LOWER SILURIC) OF THE SLATE BELT OF NEW YORK

| Formation | Slate belt of New York | Canada | Great Britain | Scandinavia (Tullberg) | Other regions |
|---|---|---|---|---|---|
| Lorraine | Zone with Dipl. foliaceus, Coryn. curtus and Lorraine fossils (Waterford) | Lorraine beds | Zone with Dicell. anceps (Upper Hartfell shales) upper Caradoc of Shropshire with Dipl. foliaceus etc. | Zone with Dipl. *sp. nov.* | Upper Maquoketa shales (Ohio and Mississippi valleys) |
| Utica | Zone with Dipl. quadrimucronatus, D. foliaceus, D. pusillus, Coryn. curtus, Triarthrus becki etc. (Rural cemetery, etc.) | Utica beds with Dipl. quadrimucronatus (Quebec etc.) and Leptogr. flaccidus (Lake St John) | Zone with Dicell. complanatus (Upper Hartfell) | Zone with Dicell. complanatus | Dd 5 of Bohemia with Dipl. pristis |
| | Transitional zone with Climacogr. caudatus, Cryptogr. tricornis, Triarthrus becki etc. (Mechanicville, Van Schaick island) | | Zone with Pleurogr. linearis, Dipl. quadrimucronatus, etc. (Lower Hartfell) | Zone with Dipl. quadrimucronatus | Lower Cincinnati, lower Maquoketa shales (Ohio valley) |
| Trenton | ? Upper Dicellogr. zone (Lansingburg power-house) | Upper Dicell. zone (Quebec and Magog, Gurley) (=zone without Coenogr. gracilis Lapw.) | Zone with Dicranogr. clingani (Lower Hartfell) | Zones with Climacogr. vasae, Dicranogr. clingani etc. | Shale of Gembloux (Ardennes) with Climacogr. caudatus, C. styloideus, and sandstone of St Germain-sur-Ile with Dipl. foliaceus and D. angustifolius |
| | Zone with Dipl. amplexicaulis (Troy) | | Zone with Climacogr. wilsoni (Lower Hartfell shales, Moffat etc.) | | |
| | Lower Dicellogr. zone (Normanskill beds) | Lower Dicell. zone (Quebec etc. Gurley) (=zone with Coenogr. gracilis Lapworth) | Zone with Coenogr. gracilis (Lapworth) Lowest Moffat beds, Glenkiln shales | Zone with Coenogr. gracilis | Shale with Coenogr. gracilis of Victoria, Australia. Shales of Arkansas |
| Chazy | | Beds of Mystic (Gurley) | | | ? Graptolite shales of Kicking Horse pass, and Dease river, British Columbia (Gurley) ? shales of Nevada |
| | Zone with Dipl. dentatus and Cryptogr. antennarius (Deep kill) | Point Levis zone (Gurley) | Ellergill beds (Elles) (= Llanvirn, Elles) | Zones with Glossograptus and Didymogr. geminus | Graptolite shales of Arkansas and Nevada |
| | Transitional subzone (Mt Moreno) | | | | |
| Beekmantown | Zone with Didymogr. bifidus and Phyllogr. anna (Deep kill) | St Anne zone (Lapworth and Gurley) Graptolite shales of Newfoundland, Division P (Billings) | Upper Tet. zone (Skiddaw slates, Elles) Upper Arenig beds of Scotland and Wales | Zone with Phyllogr. typus and Didymogr. bifidus | Shales of Cabrières, France. Dd 1 of Bohemia with Didymogr. bifidus. Auriferous shales of Victoria, Australia |
| | Zone with Tetr. (Deep kill) subz. *b* Goniogr. subzone | Main Point Levis zone (Gurley) | Lower Tet. and Dich. zones (Skiddaw slates, Elles) Middle Arenig graptolite beds of Scotland and Wales | Tetragraptus shales | Shales of Huy-Statte and Sart-Bernard (Ardennes) with Phyllogr. Dich. and Tet. Auriferous shales of Victoria, Australia |
| | " *a* Clonogr. subzone | | | | |
| Top of Upper Cambric | Zone with Dictyonema flabelliforme (Schaghticoke etc.) | Dict. flabelliforme zone Gaspé (Lapworth), St John (Matthew) | Dict. flabelliforme zone in Upper Lingula flags of Wales | Dict. flabelliforme zone Christiania, Scania, Bornholm, Oesel | Dict. flabelliforme zone Esthonia (Russia), Belgium |
| Middle Cambric | No graptolites | No graptolites | No graptolites | No graptolites | No graptolites |

Llandeilo
Caradoc
Arenig
Middle Graptolite schists
Lower Graptolite schists

correlation table of zones in New York, p.575]. To the Trenton were referred the typical Normanskill or lower Dicellograptus fauna, the lower Dicellograptus fauna of Mt Olympus at Troy, which contains some differing elements and the Diplograptus amplexicaulis fauna. The Utica formation was found to be represented by four different faunal associations: that of Mechanicville, which contains, besides the typical Utica fossils, Conularia trentonensis and Climacograptus caudatus, a form hitherto known only from Europe as being associated with the equivalent of the Normanskill fauna; the Utica fauna of Van Schaick island, which has Cryptograptus tricornis, another Normanskill form, as an element; the typical Utica fauna of Rural cemetery, etc.; and the Upper Utica fauna of the old Dudley observatory site, etc. The first two faunas are evidently transitional to the Trenton. A fuller account of the faunas of these zones and a discussion of their relations to European faunas will be given after a renewed and more detailed study, in a subsequent memoir.

In another publication [1902] the writer has announced the discovery of the Quebec (Levis) graptolite fauna at the Deep kill in the "Hudson river shales" of New York, and of its division into three well defined zones, which in their faunal constitution exactly correspond to the homotaxially successive European zones. These zones were correlated by the writer with the Beekmantown or Calciferous beds of New York, the uppermost being considered as possibly of Chazy age. It is this locality at the Deep kill which, yielding an extremely rich fauna in an exceptionally excellent state of preservation, has furnished the larger portion of the material for this memoir.

As we have in the paper mentioned given a full account of the Canadian and European equivalents of the Deep kill zones and of the geographic distribution of the faunas represented there, we refer here for all details to that publication and to the correlation table [p.575] of the zones and the table of the distribution of the species, appended to this chapter, restricting ourselves in this place to a short characterization of the zones.

The presence in New York State of the Dictyonema flabelliforme zone, so well known in Europe as characterizing the upper limit

of the Cambric, has also been announced lately by the present writer [1903]. The taxonomic position and distribution of this zone — also found in "Hudson river shales" — has been discussed in detail in the paper mentioned. It will therefore suffice briefly to review here the more important facts.

*a* **Zone with Dictyonema flabelliforme.** This zone has been found by the writer to be very well exposed at the falls of the Hoosic river in the village of Schaghticoke, Rensselaer co. N. Y. Its fossils are finely preserved in the beds exposed at Schaghticoke, and complete series of growth stages of the characteristic graptolites [pl.1] were secured at this locality. Its lithologic characters, which are similar to those of the Deep kill beds of Beekmantown age, can also be well studied at the falls, but the adjoining formations are not exposed there. The characteristic graptolites of the beds are Dictyonema flabelliforme Eichwald and Staurograptus dichotomus Emmons (Clonograptus proximatus Matthew), both in several varieties.

The limitation of the graptolite fauna to hardly more than two forms, the first representative of the long persistent genus Dictyonema and the second a pronounced synthetic form, Staurograptus, seems to be everywhere characteristic of this zone; for in Canada, where it was recognized at nearly the same time by Dawson and Lapworth in the slates trending along the south shore of the lower St Lawrence, these are the only graptolites cited. In the St John (N. B.) basin, where the vertical range of Dictyonema has been carefully studied by Matthew, these are the principal graptolites, and the species of Bryograptus cited are probably all referable to one of these forms [*see* p.616].

In Europe, the zone is considered as marking in Scandinavia, where it is widely distributed, the closing stage of the Cambric. Here also Dictyonema flabelliforme is associated with a species of Clonograptus that is similar to ours, and probably also with a few representatives of Bryograptus, which is another synthetic genus. The Dictyonema zone has been further recognized in Esthland, Oesel, Bornholm, Belgium, Wales, western England and Ireland. Brögger has demonstrated that the zone is also in Great

Britain to be regarded as marking the boundary between the Cambric and Siluric eras.

From the material collected by the geologists who have been engaged in mapping the slate belt of New York and Vermont, I infer that both Dictyonema flabelliforme and Staurograptus dichotomus are also present at other localities in the slate belt of New York, notably in the region of Granville in Washington county [*see* localities under Dictyonema flabelliforme, p.601]. The fact that almost without exception only the more common early growth stages had been collected, prevented the recognition of the presence of this stratigraphically important zone in the slate belt by the paleontologist of that survey. Subsequent investigation of the outcrops of the horizon in Washington county by the present writer has brought out the fact that the Dictyonema shale is found infolded, northward from the Hoosic river to and beyond the Vermont boundary, between the Georgian shales and slates and the basal rocks of the Lower Siluric, notably the thinly bedded limestones and intercalated shales, characteristic of the Beekmantown graptolite horizons at the Deep kill.

There is no doubt that the zone extends into Vermont, for Dictyonema flabelliforme is, for example, found at Fairhaven Vt. and probably it extends northward through that state and merges into the belt of Dictyonema slates skirting the south shore of St Lawrence bay.

An interesting fact brought out by the presence of the shale with Dictyonema flabelliforme in the slate belt of eastern New York, one which has an important bearing on the paleography of eastern North America, is that, while the contemporaneous Upper Cambric or Saratogian littoral facies of New York — the Potsdam sandstone, Greenfield limestone, at Saratoga etc. — by their included Dicellocephalus fauna were clearly deposited in the American Pacific basin, the Atlantic waters encroached close by on the present territory of the slate belt, probably along the "Levis channel" outlined by Ulrich and Schuchert, for the earlier Lower Siluric. [*See* appended chart on the distribution of the fauna with Dictyonema flabelliforme.

*b* **Tetragraptus zone.** This zone is represented at the Deep kill by two graptolite beds. While the fauna of one of the beds is largely composed of species of Didymograptus, and in the other the representatives of the genus Tetragraptus prevail, a comparison of the faunal lists of the two shows that all species occurring in the first bed are also found in the second, and that both comprise one fauna. This consists of 32 species of graptolites. Of these, 16 are restricted to this horizon. Of the remaining, the greater majority extend only into the lowest bed of the next horizon.

The most important genus, which, both by the number of its species and its individuals, gives to this zone its character, is the genus Tetragraptus, of which eight species, out of the 10 of the Deep kill section, are either restricted to this zone or clearly reach here the acme of their development. The most stately and showy forms of the genus, as T. quadribrachiatus, amii, fruticosus, serra and similis, are those found in this bed. The species of Tetragraptus found in the next horizon are either smaller mutations of these species or dwarfed species with distinct paracmic features.

Next in importance, in the number of individuals and species, is the genus Didymograptus, which, however, is represented by only five of its 14 Deep kill species in this zone, the others all being of later age. These five species all belong, as a glance at the synoptic table of the genera [p.508] will show, either to the horizontal or to the declined series. The dependent ("tuning fork") and reclined forms are still entirely absent. The horizontal series of Didymograptidae culminates in this zone and declines at its termination, entering the next zone with only one species.

The genus Phyllograptus is represented with three of its five Deep kill species in this zone, but the largest and most typical form, P. typus, is not developed till the next zone is reached.

The multiramous Dichograptidae are represented by Dichograptus octobrachiatus, which here culminates; and two of the three species of the genus Goniograptus, attain here their greatest size and frequency. It is however to be noted that the genus Clonograptus, so well represented in the Main Point Levis zone, is absent entirely and only represented by its more rigid and symmetric descendant, Goniograptus. It is, hence, very probable that the Tetragraptus zone is preceded by a subzone characterized by the

Clonograpti, which is either not exposed or not represented at the Deep kill. On the other hand, the upper Cambric synthetic genus Bryograptus extends with two species into this horizon, thereby indicating the proximity of the latter to the beginning of the graptolite reign.

Of Dendroidea we find the genera Dictyonema, Dendrograptus and Callograptus represented in this zone. Finally, the species of Dawsonia and Caryocaris, described in this paper, were also obtained from the same.

The correlation of this zone with the divisions recognized in Canada and Europe has been fully discussed before [1902]. For this reason only a short summary is here given.

The Tetragraptus zone of the Deep kill is homotaxial to a part (probably upper part) of the beds termed by Gurley the "Main Point Levis zone" of the Quebec beds. This is the zone containing the typical Quebec graptolite fauna. The same zone is probably present at St John N. B. [Matthew], and at Cow Head, Newfoundland [Billings]. The association of forms, characteristic of this horizon, is typically developed in the Middle Skiddaw slates of the Lake district, north England [Elles]. The Dichograptus bed, which there separates the lower and upper Tetragraptus bed, is probably the exact equivalent of the zone here considered. The more common species of the Tetragraptus zone are also found in the Arenig shales of St Davids, Wales, of the Shelve district in Shropshire, west England, and in the Ballantrae terrane in south Scotland. In Sweden [Törnquist and Tullberg] the fauna here under consideration is found in the "Tetragraptus shales" overlying the Ceratopyge limestone and succeeded by the Orthoceras limestone. The latter also contains in Oeland [Holm] some of the species of this zone (Tetragraptus bigsbyi and Phyll. angustifolius). In France, a number of the characteristic species of Tetragraptus and Didymograptus have been found in the graptolite schists of Boutoury near Cabrières in the Languedoc [Barrois]; and Dichograptus octobrachiatus is reported from Belgium [Malaise]. In Australia, well known Levis forms have been recorded by McCoy and Etheridge jr from various localities of Victoria.

**Subhorizon of Clonograptus cf. flexilis (Clonograptus bed).** There occurs at a locality in Rensselaer county, about 4½ miles due east from the city of Albany, in a small road metal pit on the road between Defreestville and West Sandlake, a yellowish weathering sandy slate, interbedded in light greenish and darker silicious slates, which contains a faunule that indicates the presence of a subhorizon of the Tetragraptus beds lying below the first graptolite bed observed at the Deep kill.

The faunule, which was discovered by Professor Dale (his locality 154, the material being in the National Museum) is unfortunately represented by small drifted fragments only, and the present writer has been unable to secure more favorably preserved material. It consists of

| | |
|---|---|
| Dictyonema murrayi *Hall* | c |
| Clonograptus *cf.* flexilis *Hall* | cc |
| Tetragraptus quadribrachiatus *Hall* | c |
| T. serra *Brongniart* | c |

c=common cc=very common

This faunule consists of two species of Tetragraptus, common in the Tetragraptus zone of the Deep kill, and of two species which are entirely absent at the Deep kill. One of these, Dictyonema murrayi, is recorded by Hall as occurring "in hard shales" associated with Clonograptus rigidus and two other very robust species of Dictyonema, viz D. irregularis and D. robusta. There appears, hence, also in the Quebec region an association of a Clonograptus with Dictyonemas with remarkably robust rhabdosomes. It is quite probable that both these faunules represent the same subhorizon, the exact taxonomic position of which is at present unknown. On account of the frequency of the Clonograpti, this subhorizon is however to be considered as forming a part of the Clonograptus beds and as lying in the lower part, or perhaps at the base, of the Tetragraptus beds.

*c* **Zone with Didymograptus bifidus, Phyllograptus typus and Ph. anna.** This zone at the Deep kill comprises a considerable thickness of rock, containing numerous graptolite-bearing surfaces which, in the former paper, were divided into graptolite beds 3, 4 and 5. The fauna, consisting of 28

species, is still entirely composed of Dendroidea and Dichograptidae. The prominent genera are still Tetragraptus, Phyllograptus and Didymograptus, but with new, younger elements. Four of the seven species of Tetragraptus of the preceding zone extend, as stated before, mostly in smaller mutations into this zone, and two other species, Tetragraptus clarkii and pendens, appear as new forms.

Of the Phyllograpti, P. ilicifolius, which has its acme in the preceding zone, is here rare and disappears; P. angustifolius becomes more common than before and continues throughout the zone; P. anna, which appeared in the last layer of the preceding zone, is here one of the common and characteristic fossils, but extends also into the lower part of the next zone. P. typus appears for the first time in this zone, becomes extremely common and probably ends with it. It is, hence, apparent that the genus Phyllograptus culminates in this zone.

Of the Didymograpti, the horizontal series has dwindled down to one species, D. similis. The declined series which originated in the preceding zone, continues, but develops very little strength in a specific and individual representation. The dependent series is entirely restricted to this zone and furnishes in D. bifidus and D. nanus most characteristic fossils of the same. The reclined series finally begins here with D. caduceus (gibberulus).

Of the multiramous Dichograptidae, Dichograptus octobrachiatus endures and Goniograptus disappears after developing a last, interesting species in G. geometricus. No more species of Bryograptus are found. The Dendroidea are faintly represented, among them the genus Ptilograptus with two species. With Sigmograptus the coenograptids appear on the scene.

The characteristic members of this fauna are the Phyllograpti, notably P. typus and P. anna, the dependent or "tuning fork" Didymograpti, D. bifidus and D. nanus; and a horizontal form, D. similis.

The principal species were originally reported by Hall from a place "3 miles above the River St Anne." Lapworth recognized this association in collections from the same locality and termed it the St Anne zone or zone

with Phyllograptus anna. Gurley [1896] records the occurrence of Didymograptus bifidus and Phyllograptus anna in the graptolite shale of Nevada.

In Great Britain Lapworth records a similar association from the Ballantrae rocks in south Scotland. In the Skiddaw slates the characteristic species of the zone, specially Didymograptus bifidus, Phyllograptus typus and Phyllograptus anna, are found in the upper Tetragraptus subzone which overlies the Dichograptus zone. In Scania the zone with Phyllograptus cf. typus and Didymograptus cf. bifidus forms, according to Tullberg, the highest part of the lower graptolite shale and overlies the Orthoceras limestone. But as this is also reported to contain Climacograptus and Cryptograptus, which here do not appear till the next zone, this Scanian and the Deep kill zone can not be exactly parallelized; and it is to be assumed that the typical St Anne fauna lies a little deeper and is homotaxial with a part or the whole of the Orthoceras limestone itself.

In Bohemia Didymograptus bifidus occurs in D d1γ [Perner]; and in France its occurrence and that of Rouvilligraptus richardsoni, another St Anne form, indicate the presence of the St Anne zone in the graptolite shale of Cabrières. Finally, T. S. Hall [1893] recognized the zone of Didymograptus bifidus in the auriferous shales of Victoria, Australia.

It is hence, with our present evidence, to be inferred that this zone in all lower graptolite beds of the world is directly successive to and also coextensive with the preceding Tetragraptus zone.

*d* **Zone with Diplograptus dentatus and Climacograptus? antennarius.** This zone is represented at the Deep kill by graptolite beds 6 and 7, which are separated by an interval of several hundred feet of nonexposure from the zone with Didymograptus bifidus. The writer's supposition [1902] that this interruption hides a transitional zone, of similar composition as the one, just mentioned, in Scania, with Didymograptus bifidus, Phyllograptus typus, intermingled with the graptolites of the zone of Diplograptus dentatus, has to some extent been verified by a fauna found at Mt Moreno [*see* note below].

This third Deep kill zone is characterized by the suppression of the Dichograptidae and the unheralded appearance of the axonophorous Diplograptidae, with the genera Diplograptus, Glossograptus, Trigonograptus, Climacograptus and Retiograptus, which now dominate till the end of the Lower Siluric. Accordingly, between this and the underlying zone, there has taken place a profound change, indeed the most profound change to be met with between the successive graptolite faunas; for a new subclass, the Axonophora, built on an entirely new plan, have taken possession of the field, and the Dichograptidae, hitherto holding sway in the wide areas occupied by the graptolites, persist only in a few stragglers.

*Note.* Transitional subzone. The fortunate discovery of a Phyllograptus in the shales of the Ashhill quarry at Mt Moreno near Hudson, by Prof. A. W. Grabau, has led to the finding there of a fauna which is a blending of the typical forms of the zone with Diplograptus dentatus with some species of the preceding zone. It, therefore, appears to happily fill, to a great extent, the gap in the continuity of the graptolite horizons, caused by the interruption of the outcrops between graptolite beds 5 and 6 of the Deep kill section (zones with Didymograptus bifidus and Diplograptus dentatus).[1]

The lithologic character of the beds at the Ashhill quarry is strikingly similar to that of the Deep kill beds, the bands of black graptolite shales being also intercalated in thicker masses of greenish, silicious shales.[2]

The Ashhill quarry has furnished the following forms:

| | | | |
|---|---|---|---|
| Dendrograptus *sp.* | r | D. cuspidatus *sp. nov.* | rr |
| Ptilograptus plumosus *Hall* | c | D. spinosus *sp. nov.* | r |
| Goniograptus perflexilis *sp. nov. mut* | rr | Phyllograptus angustifolius *Hall* | c |
| Tetragraptus quadribrachiatus *Hall* | rr | Diplograptus dentatus *Brong* | cc |
| T. taraxacum *sp. nov* | rr | D. laxus *sp. nov.* | c |
| T. pygmaeus *sp. nov.* | r | Climacograptus pungens *sp. nov.* | cc |
| Didymograptus forcipiformis *sp. nov.* | c | Glossograptus hystrix *sp. nov.* | r |
| D. filiformis *Tullberg* | r | Trigonograptus ensiformis *Hall* | rr |
| D. gracilis *Törnquist* | r | Retiograptus tentaculatus *Hall* | r |

[1] *See* N. Y. State Paleontol. An. Rep't 1901, pl. 2, facing p. 546.

[2] As at Mt Moreno these Lower Champlainic graptolite shales are exposed in close proximity to the Normanskill shales of Trenton age, this locality will be noticed in greater detail in a later publication in the report of the state paleontologist.

While the typical species of the zone with Diplograptus dentatus prevail, both in number of species and individuals, thus characterizing the beds as belonging to that zone, the congeries contains still a goodly number of species met only in the deeper horizons at the Deep kill, namely, Goniograptus perflexilis, Tetragraptus taraxacum and T. pygmaeus, Didymograptus filiformis and D. gracilis. The Ashhill quarry beds represent hence a very early or initial phase of the zone with Diplograptus dentatus not met with at the Deep kill, but whose existence was surmised on account of the considerable break in the rock succession at that place.[1] The Dendroidea which constitute so large a portion of the fauna of the horizon at the Deep kill are here represented only by a species of Ptilograptus and a few fragments of a Dendrograptus; but, as they also fail to be present in this zone in other countries, they may represent but a local element.

A notable feature of this faunule is the considerable number of species not observed elsewhere, or in the preceding and succeeding horizons. Some of these forms, as Didymograptus cuspidatus and D. spinosus, represent moreover peculiar types and have no closely related congeners. Other species, as Diplograptus laxus and Climacograptus pungens, which are new and very rare in the Deep kill beds with Diplograptus dentatus, appear here in great profusion. These facts characterize the fauna as constituting a distinct subzone of the zone with Diplograptus dentatus.

*e* **Some general facts of distribution of graptolites** [*see* chart]. The specific identity of so great a percentage of forms in faunas characterizing successive zones, as we find in the deeper zones of the Lower Siluric, over so vast an area as that outlined above, by the notes on the distribution of the Lower Siluric graptolites, is a fact without a parallel among the paleozoic faunas. It has a distinct bearing on several problems, notably on that of the mode of existence of the graptolites and of the distribution of land and water in the Lower Siluric time. The former problem will be discussed in the following chapter, the relation of the graptolites to paleography however is still a virgin field, promising rich fruit after a most detailed comparison of the various faunas. We can, with the present knowledge of the distribution of the graptolites, do little more than make some general statements.

[1] *See* N. Y. State Paleontol. An. Rep't 1901, p. 572.

It has been pointed out by Frech [1897, 2:88] that for the lower and middle Lower Siluric the existence of four grand marine provinces can be inferred, which were more or less separated from one another. These are the Bohemian–Mediterranean, the Baltic, the North Atlantic, and the Pacific–North American basins. The former existence and extension of these provinces is deduced from the comparative study of the horizontal distribution of the faunas, specially of their trilobite element.

The graptolites, however, are expressly excepted as passing beyond the boundaries of these basins. Indeed, we find, for instance, the Tetragraptus zone with its principal forms developed in the northwestern (St Lawrence) and northeastern (British) embayments of the north Atlantic basin, in the Baltic basin (Scandinavia), Bohemian–Mediterranean basin (southern France) and Pacific–American basin (province of Victoria, Australia, and Nevada). The same, with some exceptions, is true of the succeeding zones, at least as far as the Trenton or Normanskill fauna is concerned.

This phenomenon is explained by Frech by their pelagic or abysmal habitat in contrast to the littoral or shallow sea habitat of the provincial faunas, which consist essentially of brachiopods, mollusks and trilobites. We shall see in the succeeding chapter that, whatever may have been the mode of existence of the graptolites, for various reasons they can not be considered as having been littoral benthonic forms living in association with the representatives of the other classes mentioned, but were either pelagic or abysmal organisms. Either of the latter are, today, notable for the vastness of the territory inhabited by them, many of the former and nearly all of the latter being cosmopolitan.

While, however, the most common and characteristic species of the graptolite zones appear also to be practically cosmopolitan, a closer comparison of those homotaxial faunas which have been thoroughly studied, brings to light certain differences in the composition of the faunas which may indicate divisions of the open sea, independent of those suggested by the shallow sea organisms. We find in the Upper Cambric Dictyonema

flabelliforme zone, that, while the index fossil is present in both America and North Europe, it is associated in Europe with a species of Clonograptus (C. tenellus), while in the northwestern embayment of the Cambric Atlantic sea, Clonograptus proximatus Matthew (or Staurograptus dichotomus Emmons) appears as a vicarious form in the homotaxial St John and New York beds. Elles [1898, 463ff] concluded in regard to the Skiddaw slate fauna, that, "though it is more closely related to the fauna of the Quebec group of Canada than to that of any English beds, it is still more nearly related to the Swedish fauna; for, while of the whole 59 species, 25 are common to the Skiddaw slates and the Quebec, and only 14 common to the Skiddaw slates and the two other English areas, no less than 34 species are common to the beds of Sweden and the Skiddaw slates." While, with further elaboration, undoubtedly still more forms will be found to be common to these regions, as indeed the writer's investigation of the New York graptolites distinctly shows, new forms are being discovered which are not known to the other territories, and thus the differences in the composition of the equivalent faunas will be maintained. These differences are probably of a provincial or regional nature, as the closer approximation of the regionally adjoining Swedish and Skiddaw faunas indicates.

A still wider difference appears to exist between the Lower Siluric graptolite faunas of Bohemia and northern Europe, which have but very few species in common. This coincides with the great difference of the littoral faunas of the Bohemian and Scandinavian Lower Siluric seas, belonging respectively to the Bohemian and Baltic basins. On the other hand, the graptolite fauna of Cabrières in southern France, which also belongs to the Bohemian–Mediterranean basin, contains a greater number of the more important forms of the Scandinavian or Skiddaw faunas. [*See* appended chart on the distribution of the Lower Siluric graptolite faunas]

Some facts concerning the distribution of the Lower Siluric graptolites are entirely at variance with the distribution of the land and water masses,

as it can be reconstructed for the Lower Siluric age from the study of the littoral faunas.[1] One of these is the appearance of the peculiar generic type Goniograptus with the same species, G. thureaui, in Victoria, Australia, in the south Australian sea of that age which formed presumably a southwestern embayment of the Pacific–American basin, and in the homotaxial Tetragraptus beds of Point Levis, Canada, and the Deep kill, New York, while no trace of it has been found in the corresponding European beds. The only explanation of this abnormal distribution can, in the writer's opinion, be found in the assumption that the supposed "Levis channel" of Ulrich and Schuchert had at that time not only an open connection with the northwestern (St Lawrence) embayment of the North Atlantic basin, but also at its southern terminus with the Pacific–American basin, and that oceanic currents connected the habitats of Goniograptus thureaui, at present antipodal regions. [*See* chart]

Another irregularity of distribution can be found in the appearance of the Dendroidea, with the genera Dendrograptus, Dictyonema, Callograptus and Ptilograptus, in great force at certain localities, while they are absent in homotaxial beds at others. Thus Lapworth and Hopkinson [1875, p.635] enumerate from the graptolite beds on Ramsey island, Wales, 10 Dendroidea to only six Graptoloidea. From the whole St Davids district they record 15 Dendroidea to 20 Graptoloidea, while the Dendroidea are entirely absent in the corresponding beds of the English Lake district, and are rare in the homotaxial beds of the Quebec region. They are, further, extremely prominent in species and individuals in the third Deep kill zone, that of Diplograptus dentatus [*see* table of distribution of species, p.504], while they are absent in the same zone at Point Levis and in the Lake district; and are hardly represented at Mt Moreno. The peculiarly local distribution of this class of graptolites would seem to suggest a mode of existence different from that of the other members of the group [p.514].

[1] *See* Frech. Lethaea palaeozoica, v.1, chart 2.

SYNOPTIC TABLE OF THE DISTRIBUTION OF THE CAMBRIC

(r = rare; rr = very rare; c = common;

| | Dictyonema bed of New York | Deep Kill | | | | | | Other localities in New York and Vermont |
|---|---|---|---|---|---|---|---|---|
| | | Zone of Tetragraptus | | Zone of Didy. bifidus | | Zone of Dipl. dentatus | | |
| | | Bed 1 | Bed 2 | Bed 3 | Bed 5 | Bed 6 | Bed 7 | |
| 1 Dictyonema flabelliforme *Eichwald* | cc | ... | .... | ... | ... | ... | ... | ..... |
| 2 D. rectilineatum *Ruedemann* | ... | ... | ... | ... | ... | ... | r | ..... |
| 3 D. furciferum *Ruedemann* | ... | ... | r | r | ... | ... | ... | ..... |
| 4 D. murrayi *Hall* | ... | ... | ... | ... | ... | ... | ... | 17 |
| 5 Desmograptus cancellatus *Hopkinson* | ... | ... | .... | ... | ... | ... | c | ..... |
| 6 D. intricatus *Ruedemann* | ... | ... | .... | ... | ... | ... | c | ..... |
| 7 Dendrograptus flexuosus *Hall.* | ... | ... | c | r | ... | ... | ... | ..... |
| 8 D. fluitans *Ruedemann* | ... | ... | r | ... | ... | ... | ... | ..... |
| 9 D. succulentus *Ruedemann* | ... | ... | .... | ... | ... | ... | c | ..... |
| 10 Callograptus salteri *Hall* | ... | r | c | ... | r | ... | ... | ..... |
| 11 C. *cf.* diffusus *Hall* | ... | ... | r | ... | ... | ... | r | ..... |
| 12 Ptilograptus plumosus *Hall* | ... | ... | .... | ... | ... | ... | rr | (c)[18] |
| 13 P. geinitzianus *Hall* | ... | ... | .... | rr | ... | ... | ... | ..... |
| 14 P. tenuissimus *Hall* | ... | ... | ... | rr | ... | ... | ... | ..... |
| 15 Bryograptus lapworthi *Ruedemann* | ... | c | cc | ... | ... | ... | ... | ..... |
| 16 B. pusillus *Ruedemann* | ... | ... | rr | ... | ... | ... | ... | ..... |
| 17 Staurograptus dichotomus *Emmons* | cc | ... | .. | ... | ... | ... | ... | 5 |
| 18 Clonograptus *cf.* flexilis *Hall* | ... | ... | .... | ... | ... | ... | ... | 17 |
| 19 Goniograptus thureaui *McCoy* | ... | ... | cc | c | ... | ... | ... | ..... |
| 20 G. geometricus *Ruedemann* | ... | ... | r | cc | ... | ... | ... | ..... |
| 21 G. perflexilis *Ruedemann* | ... | ... | cc | r | ... | ... | ... | ..... |
| 22 Loganograptus logani *Hall* | ... | ... | ?cc | ... | ... | ... | rr | ..... |
| 23 Dichograptus octobrachiatus *Hall* | ... | rr | cc | r | ... | ... | rr | ..... |
| 24 Tetragraptus quadribrachiatus *Hall* | ... | ... | cc | r | ... | ... | rr | (rr)[17, 18] |
| 25 T. amii *Elles & Wood* | ... | ... | c | ... | ... | ... | ... | ..... |
| 26 T. fruticosus *Hall* | ... | c | cc | cc | ... | ... | ... | ..... |
| 27 T. clarkii *Ruedemann* | ... | ... | .... | c | ... | ... | ... | ..... |
| 28 T. pendens *Elles* | ... | ... | .... | r | ... | ... | ... | ..... |
| 29 T. serra *Brongniart* | ... | r | c | ... | ... | ... | ... | 17 |
| 30 T. similis *Hall* | ... | ... | cc | c | ... | ... | ... | ..... |
| 31 T. taraxacum *Ruedemann* | ... | ... | r | ... | ... | ... | ... | (r)[18] |
| 32 T. pygmaeus *Ruedemann* | ... | ... | c | r | ... | ... | ... | (r)[18] |
| 33 T. lentus *Ruedemann* | ... | ... | .... | r | ... | ... | ... | ..... |
| 34 Didymograptus extensus *Hall* | ... | ... | cc | ... | ... | ... | ... | ..... |
| 35 D. nitidus *Hall* | ... | c | c | ... | ... | ... | ... | ..... |
| 36 D. patulus *Hall* | ... | cc | cc | ... | ... | ... | ... | ..... |

[1] Cape Breton island; Cape Rosier, Gaspé. [2] Also in Ostrogothia, Vestrogothia and Esthonia, Russia; Bornholm and Ireland. [3] Gros Maule, Canada. [4] Orleans island [Ami]. [5] Rensselaer county, N. Y. [Emmons]. [6] Cape Rosier zone, Canada [Lapworth]. [8] Also Orthoceras limestone of Oeland. [9] Also Vestrogothia. [10] Also in South Shropshire (Shelve district). [11] Kiltrea near Ennis-

AND LOWER CHAMPLAINIC GRAPTOLITES OF NEW YORK

cc = very common; x = present)

| Levis, Quebec | | | | St John Division 3 | | | | | | Arenig Lake district North England | | | | | Christiania | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Main Point Levis zone | Phyllograptus anna zone | Point Levis zone | Miscellaneous | b & c | d | Newfoundland | Arkansas (A) or Nevada (N) | Arenig, South Scotland | Lower Skiddaw | Middle Skiddaw | Upper Skiddaw | Upper Lingula flags, Wales | Arenig, St Davids etc., Wales | 2d | 3b Phyllograptus shale | Scania | Dalarne | Belgium | Bohemia | France (Cabrières) | Australia |
| | | | [1] | x | | | | | | | | x | | x | | x[2] | | x | | | |
| | | | | | | | | | | | | | x | | | | | | | | |
| x | | | | | | | | | | | | | x | | | | | | | | |
| x | | | [3] | | | | | | | | | | x | | | | | | | | |
| | | x | | | | | | | | | | | x | | | | | | | | |
| x | | | [4] | | | x | | | | | | | | | | | | | | | |
| x | | | | | | | | | | | | | | | | | | | | | |
| | | | [6] | x | | | | | | | | | | | | | | | | | x |
| x | | | | | | | | | | | | | | | | | | | | | |
| | | x | [4] | | x | | | | | x | | | x | | x | ? | x | x | | | x |
| x | | | | | | | | x | | x | | | x | | x | x | x | | | x | x |
| x | | | | | x | | | x | | x | | | x | | | | | | | | |
| x | x | | [4] | | | x | | x | | x | | | | | x | x | | | | | x |
| | | | | | | | | | | x | | | x | | x | x[8] | | | x | | x |
| x | x | | | | | | | x | | x | | | | | x | x[9] | | | | | |
| x | | | | | | | | | | | | | | | | | | | | | |
| ?x | | | | | x | | | | | x | | | x[10] | | ?x | | | | | x | x |
| x | | | | | x | | | | | | | | | | | | | | | | |

worthy, Ireland. [12] Also New Zealand. [13] Also in Ireland. [14] In uppermost layers. [15] Chaudière river, Canada. [16] Top of Phyllograptus zone. [17] Sandy shale between Defreestville and West Sandlake, N. Y. [18] Mt Moreno near Hudson N. Y. (lower part of zone of Dipl. dentatus)

SYNOPTIC TABLE OF THE DISTRIBUTION OF THE CAMBRIC
(r = rare; rr = very rare; c = common;

| | Dictyonema bed of New York | Deep Kill | | | | | | Other localities in New York and Vermont |
|---|---|---|---|---|---|---|---|---|
| | | Zone of Tetragraptus | | Zone of Didy. bifidus | | Zone of Dipl. dentatus | | |
| | | Bed 1 | Bed 2 | Bed 3 | Bed 5 | Bed 6 | Bed 7 | |
| 37 D. similis *Hall* | ... | ... | ... | r | c | ... | ... | ..... |
| 38 D. acutidens *Lapworth* | ... | ... | ... | rr | ... | ... | ... | ..... |
| 39 Didymograptus cuspidatus *Ruedemann* | ... | ... | ... | ... | ... | ... | ... | (rr)[18] |
| 40 D. gracilis *Törnquist* | ... | ... | ... | c | ... | ... | ... | (r)[18] |
| 41 D. ellesi *Ruedemann* | ... | ... | ... | c | ... | ... | ... | ..... |
| 42 D. nicholsoni *var.* planus *Elles & Wood* | ... | ... | r | ... | ... | ... | ... | ..... |
| 43 D. törnquisti *Ruedemann* | ... | ... | ... | r | ... | ... | ... | ..... |
| 44 D. filiformis *Tullberg* | ... | ... | r | ... | ... | ... | ... | ..... |
| 45 D. bifidus *Hall* | ... | ... | ... | cc | cc | ... | ... | .... |
| 46 D. nanus *Lapworth* | ... | ... | ... | ... | x | ... | ... | ..... |
| 47 D. caduceus *Salter* | ... | ... | ... | ... | c | ... | ... | ..... |
| 48 D. caduceus *Salter, mut.* nana | ... | ... | ... | ... | ... | ... | c | ..... |
| 49 D. forcipiformis *Ruedemann* | ... | ... | ... | ... | ... | ... | ... | (c)[18] |
| 50 D. incertus *Ruedemann* | ... | ... | ... | ... | ... | ... | rr | ..... |
| 51 D. spinosus *Ruedemann* | ... | ... | ... | ... | ... | ... | ... | (r)[18] |
| 52 Phyllograptus typus *Hall* | ... | ... | ... | c | cc | ... | ... | ..... |
| 53 P. ilicifolius *Hall* | ... | r | cc | ... | r | ... | ... | ..... |
| 54 P. angustifolius *Hall* | ... | rr | r | c | ... | c | ... | (c)[18] |
| 55 P. anna *Hall* | ... | ... | r[14] | cc | c | c | ... | ..... |
| 56 Temnograptus noveboracensis *Ruedemann* | ... | ... | c | ... | ... | ... | ... | .... |
| 57 Sigmagraptus praecursor *Ruedemann* | ... | ... | ... | rr | ... | ... | ... | ..... |
| 58 Strophograptus trichomanes *Ruedemann* | ... | ... | ... | ... | ... | ... | c | ..... |
| 59 Diplograptus dentatus *Brongniart* | ... | ... | ... | ... | ... | r | cc | (cc)[18] |
| 60 D. inutilis *Hall* | ... | ... | ... | ... | ... | ... | r | ..... |
| 61 D. longicaudatus *Ruedemann* | ... | ... | ... | ... | ... | ... | rr | ..... |
| 62 D. laxus *Ruedemann* | ... | ... | ... | ... | ... | ... | c | (c)[18] |
| 63 Glossograptus hystrix *Ruedemann* | ... | ... | ... | ... | ... | ... | r | (r)[18] |
| 64 G. echinatus *Ruedemann* | ... | ... | ... | ... | ... | ... | rr | .... |
| 65 Trigonograptus ensiformis *Hall* | ... | ... | ... | ... | ... | r | cc | (r)[18] |
| 66 Climacograptus ? antennarius *Hall* | ... | ... | ... | ... | ... | ... | cc | (c)[18] |
| 67 C. pungens *Ruedemann* | ... | ... | ... | ... | ... | ... | r | (cc)[18] |
| 68 Retiograptus tentaculatus *Hall* | ... | ... | ... | ... | ... | c | r | (r)[18] |
| 69 Dawsonia monodon *Gurley* | ... | c | c | ... | ... | ... | ... | ..... |
| 70 D. tridens *Gurley* | ... | ... | c | ... | ... | ... | ... | ..... |
| 71 Caryocaris curvilineatus *Gurley* | ... | ... | c | ... | ... | ... | ... | ..... |

[1] Cape Breton island; Cape Rosier, Gaspé. [2] Also in Ostrogothia, Vestrogothia and Esthonia, Russia; Bornholm and Ireland. [3] Gros Maule, Canada. [4] Orleans island [Ami]. [5] Rensselaer county, N. Y. [Emmons]. [6] Cape Rosier zone, Canada [Lapworth]. [8] Also Orthoceras limestone of Oeland. [9] Also Vestrogothia. [10] Also in South Shropshire (Shelve district). [11] Kiltrea near Ennis-

**AND LOWER CHAMPLAINIC GRAPTOLITES OF NEW YORK** (*concluded*)

cc = very common; x = present)

| Levis, Quebec | | | | St John Division 3 | | | | | | Arenig Lake district North England | | | | | Christiania | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Main Point Levis zone | Phyllograptus anna zone | Point Levis zone | Miscellaneous | b&c | d | Newfoundland | Arkansas (A) or Nevada (N) | Arenig, South Scotland | Lower Skiddaw | Middle Skiddaw | Upper Skiddaw | Upper Lingula flags, Wales | Arenig, St Davids etc., Wales | 2d | 3b Phyllograptus shale | Scania | Dalarne | Belgium | Bohemia | France (Cabrières) | Australia |
| | x | | | | | | | | | | | | $x^{10, 11}$ | | x | ? $x^{9}$ | | | | | |
| | | | | | | | | | | | | | $x^{10}$ | | | | | | | | |
| | | | | | | | | | | | | | | | | | x | | | | |
| | | | | | | | | | | x | | | | | | | | | | | |
| | | | | | | | | | | | x | | | | | | | | | | |
| | | | | | | | | x | | | | | | | x | x | ? | | | | |
| | x | x | | | | | N | x | | x | x | | $x^{10, 13}$ | | x | x | | | x | x | |
| | | | | | | | | | | x | x | | x | | | | | | | | |
| | | | | | | | | | | x | | | x | | x | $x^{9}$ | | | | | $x^{12}$ |
| | | | | | | | | | | | | | | | | | | | | | |
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| | | | | | | | | | | | | | | | | | | | | | |
| x | | | | | | x | ? A | x | | x | | | -- | | x | x | | x | | | x |
| x | | | | | | | | | | x | | | | | | | | | | | |
| x | x | | | | | | | | | x | | | | | x | $x^{8}$ | | | | | |
| | x | | 15 | | | | A, N | x | | x | | | | | | | | | | | |
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| | | | | | | | | | | | | | | | | | | | | | |
| | | x | | | | | A | | | | x | | $x^{10}$ | | | $x^{16}$ | | | | | |
| | | x | | | | | | | | | | | | | | | | | | | |
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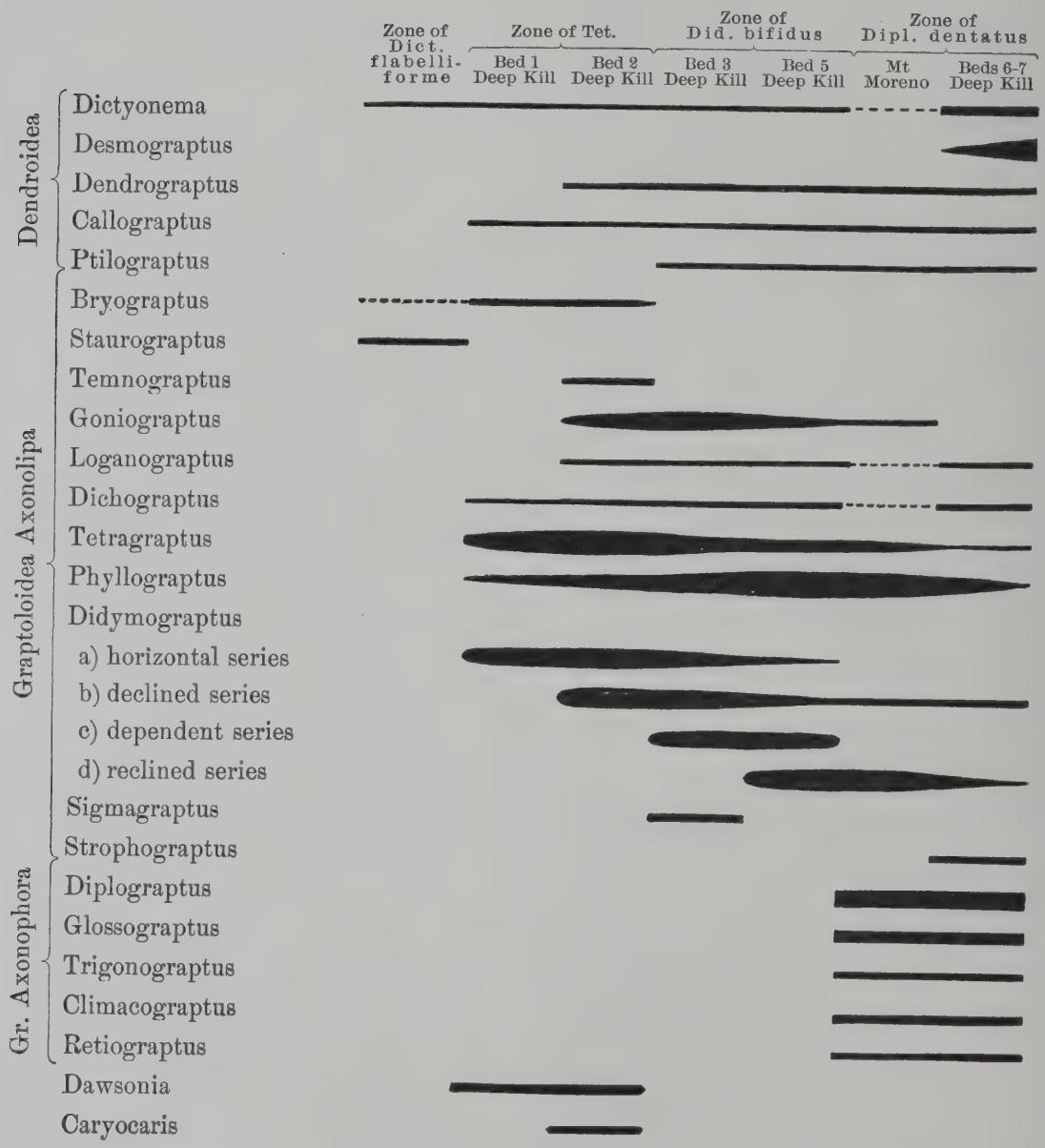
| | | | | | | | | | | | | | | | | | | | | | |
| | | x | | | | | A | | | | x | | x | | | | | | | | |
| | | x | | | | | A | | | | x | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | | |
| | | x | | | | ? x | | | | | | | | | | | | | | | |
| x | | | | | | | | | | | | | | | | | | | | | |
| x | | | | | | | | | | | | | | | | | | | | | |
| x | | | | | | | | | | | | | | | | | | | | | |

worthy, Ireland. [12] Also New Zealand. [13] Also in Ireland. [14] In uppermost layers. [15] Chaudière river, Canada. [16] Top of Phyllograptus zone. [17] Sandy shale between Defreestville and West Sandlake, N. Y. [18] Mt Moreno near Hudson N. Y. (lower part of zone of Dipl. dentatus).

SYNOPTIC TABLE OF THE RANGE OF THE GENERA OF THE CAMBRIC AND LOWER CHAMPLAINIC OF NEW YORK



### 6 Mode of existence

The problem of the mode of existence of the graptolites has as a rule been touched but incidentally by investigators, and the views entertained by various authors regarding its solution differ widely. Moreover, as with but few exceptions, only fragments of the rhabdosomes are known, and these were taken for the whole colonies, these views are mostly based on erroneous conceptions of the rhabdosomes.

Hall [*Quebec Grapt.* p.38,39], though using the term "radicle" for the sicula, considered the Graptoloidea free floating organisms, as appears from the following statement: "For all those species with a single range of cellules, as well as for some with a double range, including Retiolites, Retiograptus, and Phyllograptus, I conceive that we have already shown a similar plan of development and a uniform mode of existence; and we are constrained to believe that all these forms, in their mature condition, were free floating bodies in the Silurian seas." In regard to the Dendroidea he "inferred their attachment either to the sea bottom or to foreign bodies," but adds that he has never observed them attached, largely because there do not occur in the graptolite beds any other bodies to which they could be attached; but neither has any evidence been found of the attachment of the Dictyonemas which in the Niagara, Upper Helderberg and Hamilton groups occur in association with large numbers of other fossils. Richter, Scharenberg and Geinitz expressed the opinion that the graptolites were attached by their Fuss (sicula), or had this lower extremity plunged into the mud or sand [Geinitz]. Nicholson held that some (as Didymograptus) were attached, and others (as Monograptus and Coenograptus) were free. Herrmann assumes "that all graptolites provided with a sicula were not attached bodies," basing his view on the tapering of the sicula into a fine point or nema or its supposed disappearance. He leaves the question open, whether they were inserted into the mud with this free end or kept at small depths "like a Cartesian diver," while, like all other graptologists, he considers the arborescent forms (Dendroidea) as having been attached.

Jaekel sketched the mode of existence of the graptolites very decidedly in 1889, asserting that they formed meadows at the sea bottom and fixed themselves with a network of root fibers. His arguments for this conception were, that the graptolites can not have been free-swimming for the reason that their colonies were too heavy to be carried by the water; that they would have had either to move by concerted movements of the zooids, against which the independence of the thecae and of their apertures, and the form of the rhabdosomes militate, or that they would have had to use a hydrostatic apparatus. In the latter case, the central disk would have to be regarded as that organ; it would then, however, have been floating above the colony and the thecae would have been directed downward, which is considered as unnatural.

The same conception of the mode of existence of the graptolites was attained by Wiman [1895, p.68] by the following considerations. The graptolite beds can not have been deposited in the shallow littoral regions on account of their thin bedding, they can not be supposed to be deep sea deposits, and are hence, by exclusion, deeper littoral deposits. The graptolites were however not pelagic, as the occurrence in these beds of deeper origin might suggest, for then they would occur as frequently in limestones as in shales; further, on account of the great similarity of their external form, they all must have had the same mode of existence and belonged to the same fauna, but the combined length and stiffness of the nemacaulus, which is still increased by the virgula, as well as the adhering disk of some forms, point to an upright position of the rhabdosome.

The present writer discovered in the Utica shale complete synrhabdosomes of Diplograptus and, observing a central bulb, or cystlike organ, described this as having probably had the function of a "float" [1894, p.225], basing his assertion of the floating habit of this genus of graptolites on the great length and thinness of the nemacaulus supporting the rhabdosome, the absence of attached specimens among the numerous synrhabdosomes observed, and the facts of the distribution of the graptolites.

Gürich [1896, p.960] had, at the same time, by his study of the Polish graptolite horizons arrived at the conclusion that the monograptids, populating these horizons, had belonged to the plankton. He cites as his arguments the geologic distribution of the graptolites, their mode of preservation in the rock, their appearance in heteropic beds and their accumulation in such beds, which for other reasons also must be considered as formations of the deeper sea. He finds a verification of his views in the writer's observations on Diplograptus.

The former mode of existence of fossil marine animals has been thoroughly studied by Johannes Walther [1897]. The graptolites have thereby excited his special interest, because, as a group of most excellent index fossils, they must have lived under conditions greatly different from those indicated by the mode of occurrence of the majority of fossils. He finds that they were most pronounced facies animals, being bound to thinly bedded, carbonaceous shales. The connection of the graptolites with a distinct facies, it is stated, would argue for the conclusion that the graptolites belonged to the sessile benthos, being attached in some fashion to the bottom of the sea, as has been claimed by Jaekel. The author rejects this conclusion on the ground that in that case they should occasionally be found to pass the bedding planes, while, as he was informed by Professor Lindström, they are never found in that position in the Swedish graptolite shales, the sandstones or limestones. The clue to the solution of the apparent contradiction of the occurrence of the graptolites in a characteristic facies and on the bedding planes was, as he states, furnished to him by Professor Lapworth, who prepared a statement of his views, published in the same paper.

We can not refrain from enumerating here the important conclusions of this authority on matters referring to graptolites.

Lapworth found, during his extended researches of the English graptolitiferous beds, that the typical or rhabdophorous graptolites occur in all sediments, but are most frequent in such deposits as possess a strong admixture of carbonaceous matter, and that the number of genera, species and individuals increases in direct proportion (1) to the quantity of carbonaceous matter,

(2) to the fineness of the sediment, and (3) to the length of the time of deposition. He concludes, further, that the graptolites did not produce the carbonaceous matter of the black shales by their decomposition, for they are never found as partly decayed rhabdosomes, which pass into the surrounding carbonaceous matter. That they did not live as sessile benthos attached to the bottom of the sea can be inferred from the fact that they never pass vertically from one bed to the other, but are always spread out as if they had slowly settled in tranquil water.

The distribution of the typical black graptolite shales of Great Britain shows further that they preserve their strikingly thin bedding and fine grained character over enormous distances in a northeasterly and southwesterly strike, but that, when traced in the direction from northwest to southeast, they rapidly change into coarser sediments and graywackes, or into deposits of shallow water with surface currents. This northeast-southwest extension is now, for certain reasons, to be considered as running parallel to the protozoic coast line, and the graptolite beds in England are hence dependent, in a sense, on the old coast lines of that period. While the absence of clastic material in the Moffat shales proves their deposition in deep water distant from the coast, the black graptolite shales embedded in the contemporaneous coarser sediments of Girvan and Wales were deposited at a much faster rate. Hence the same black, fine, muddy sediments can be formed in deeper and shallower water, and not the *depth* but the *tranquillity* of the water is the most essential factor.

As the graptolites did not furnish the cellulose material for the carbonaceous shales, it is to be inferred that this was derived from plants. On account of the scarcity of land plants in the lowest Ordovicic, there remains, by exclusion, the derivation of the carbonaceous matter from drifting seaweeds. The enormous masses of Sargassum which, torn from the coasts, continue to live while drifting in the oceans as pseudoplankton, are cited as a recent example for comparison.

The bands of carbonaceous beds would then, according to Lapworth,

represent a zone between the agitated bottom where coarser sediments are deposited and the dead water of the deep sea.

Lapworth infers further, from the writer's observations on Diplograptus and other facts, that the nema of every sicula was originally an organ of attachment, either to a "central organ" or to a foreign body. He has found, that in the Dendroidea, to which also Dictyonema belongs, all transitions occur from the stem of the typical Dendroidea to the threadlike nema. In the latter case they must have been suspended like a bell at the end of a rope from the supporting object. They were now, according to Lapworth, attached to floating objects, as seaweeds; and this is held to explain both their constant appearance in carbonaceous sediments and their world-wide distribution. In support of this hypothesis are further cited the facts that only the siculate and funiculate graptolites swarmed in such multitudes over the world, while the sessile Dendroidea are by no means common; that further the first profuse appearance of graptolites, in the upper Cambric Dictyonema fauna, is that of siculate suspended forms. These, Lapworth argues, are the first types in which the originally benthonic mode of existence has changed into a pseudoplanktonic; and it is suggested that they thus escaped from some creeping enemy.

With this change in the mode of existence was connected the complete reversion in the position of the whole rhabdosome which gradually took place during the development of the various graptolite series.[1] Its purpose was to restore to the thecae their original ascending direction.

The distinguished author concludes by stating that it can be considered as established, that some graptolites, specially the Dendroidea, were attached during their lifetime to fixed objects, that possibly others belonged to the plankton proper, but that the majority of the typical graptolites lived as pseudoplankton.

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[1]This interesting and significant reversion is fully described in the chapter on the phylogeny of the graptolites [*see* p.530].

Frech [*Lethaea palaeozoica*, 1:684] considers the graptolites as gregarious, free planktonic organisms. His conception is based on the present writer's observations on Diplograptus, while Lapworth's views, just cited, had not been published and have therefore not been taken into consideration. Of special interest is Frech's discussion of certain hitherto problematic features of the graptolite structure in the light of a possible planktonic existence [*ibid.* p.552]. The semicircular expansions of the distal ends of the rhabdosomes of Diplograptus physophora, formerly described by Lapworth as air cells, the distal "discus" of Monograptus pala and the well known distal expansions between strong spines of Climacograptus bicornis are considered as steering rudders used in the rising and sinking of the synrhabdosomes. The rudderlike broadening of the entire stipe of the later Diplograptidae (Cephalograptus) and the alate pellicle of Dicellograptus divaricatus var. rigida[1] are also held to have subserved the same function. The solid axis of the rhabdosomes, in which Wiman saw an argument against their possible suspension, is explained as having served to strengthen the rudder pole.

In undertaking to present our own views on this important problem of the mode of existence of the graptolites, we will state at the outset that our observations agree fully with the facts brought forward by Lapworth, and that we believe his hypothesis furnishes a very plausible explanation for numerous characters of at least one large group of graptolites. It appears further that, in the discussion of the problem before us, the three principal groups of this class, which succeed each other in time of appearance, namely the Dendroidea, the Axonolipa or the Graptoloidea without solid axes and the Axonophora or forms with axes [p.546], should be treated separately.

The Dendroidea approach in their habit most closely to certain recent Hydrozoa; they have been observed to possess sometimes a distinct network

[1]The New York State Museum contains specimens belonging to this genus in which a continuous pellicle is stretched between the entire distal part of the two branches.

of hydrorhiza or adhesive threads such as the mature hydroids have. They were hence, at least in these cases, firmly attached in an upright position to the sea bottom or to other bodies, probably sessile seaweeds. Hence their localized appearance. Other Dendroidea, as Dictyonema flabelliforme, have no doubt, at least at certain stages, been suspended, as the relation of their long thin nema to the large rhabdosome distinctly demonstrates [pl.1]. We, hence, agree with Lapworth that the Dendroidea may have been partly attached in an upright position to the sea bottom or seaweeds and partly have been suspended from seaweeds. Whether any were free floating can not now be established; but the discovery among the hydroids of free floating colonies or hydroid colonies actually moving independently, by the concerted action of the zooids, which do not differ from the sessile ones, proves that an analogous case among the Dendroidea [*see* Dictyonema flabelliforme, p.595] may be possible.

As to the rhabdosomes of the Graptoloidea or graptolites proper, Lapworth, Gürich, Frech and the present writer in former publications agree that they were suspended. Jaekel's argument, which he brought forward for a sessile mode of life, namely that the thecae would naturally be turned upward toward the food supply, can be directly used as an argument for the opposite hypothesis, as the investigations of Wiman and the present writer have since shown, that in the axonophorous graptolites the first theca reverses its original direction, and the succeeding thecae grow backward along the nemacaulus to attain this ascendant position. In regard to the Axonolipa (Dichograptidae) Lapworth has pointed out, that, on the whole, branches change their dependent position gradually into a reclined or recumbent position to attain the same result.

There remains then to be discussed only the question whether all the graptolites proper or Graptoloidea were suspended from seaweeds or all from a "float" of their own, or whether one part had adopted the former and the other the latter mode of suspension. To shorten matters, we shall begin by stating that we entertain the view that the Axonolipa were suspended from seaweeds, while the later Axonophora had proceeded

to a free or holoplanktonic mode of existence. This view is based on the following facts.

In the Axonolipa we find the rhabdosome in all cases where the proximal parts have been observed, suspended either by means of an extremely thin, distinctly flexuous nema [p.614, and pl.12] or fastened directly to a disk without the intercalation of a nema. The former mode of suspension is observed among the lighter, thin branched forms and all the younger individuals [pl.12], while the unwieldy attachment of the base of the rhabdosome to a disk occurs among the mature, heavy branched forms of larger dimensions, notably of the genera Dichograptus and Didymograptus [pl.13]. This mode of attachment is apparently well adapted to a sessile existence on the underside of floating seaweeds, which naturally will be exposed more or less to the commotion of the surface waters. The young lighter forms could favorably meet these conditions by a suspension which allowed ready yielding to the movements of the water, thus preventing their being torn from their bases. As the rhabdosomes grew heavier, a stage would be reached where the thin, flexuous nema would no longer furnish a safe attachment, and a strengthening of the same would lead to an inflexibility which would result in breaking off the basal stem in case of more violent commotions of the water. Then the nema was gradually discarded, and the rhabdosome began to hug the supporting seaweed closely. This condition is specially well shown by the horizontal Didymograpti, as D. patulus and extensus, which, while rigidly horizontal, attain a great length. In them a nema is never observed, while the central disk has been seen by the writer to be closely attached to or to surround the apical portion of the sicula [pl.13]. It is further to be noted that in the latter forms the branches did not attempt to assume a reclined direction, sought by the others; and thus voluntarily forewent the advantage of giving the thecae an upward direction, which, with the supposed close attachment to the underside of a seaweed, would have been a distinct disadvantage. It is therefore to be assumed that they were attached to the more solid portions, the stems or median parts of the leaflike

expansions of the thallus of the giant seaweeds, which would be less pliable and fluctuating with the waves.

In this connection the thick nema of Tetragraptus fruticosus [pl.10], which would seem to disagree with the foregoing remarks, deserves special notice. Complete specimens show however that this nema tapers upward into a fine thread, and that hence also these beautiful rhabdosomes were suspended, as is clearly indicated by the recurving of the branches. Moreover, in several cases the compression of the organisms has separated this apparently thick stem into two bands, indicating its hollow character. It suggests itself readily that this secondary expansion of the nema may have been filled with gas and to some extent aided in supporting the large and heavy rhabdosome. The later developed central disk of some Dichograptidae appears from the writer's observation [p.746] to have been composed of two layers, as was also suggested by Hall; and the deposition of lime between its walls described in this paper [p.746] would indicate that it probably was a hollow body, the filling of which with gas may, at times of accidental separation from the supporting seaweeds, have saved the rhabdosome from sinking to the bottom.

After the development of the Dichograptidae, and with them that of the axonolipous forms, has reached its acme in the second Deep kill zone, the axonophorous forms, represented by Diplograptidae and Climacograptidae, appear in the third zone. In these we find a number of structural departures from the Dichograptidae, which indicate a somewhat different mode of existence. These are the presence of a solid axis, which already originates in the wall of the sicula and extends into the nemacaulus, as the present writer has shown [1896, pl.2]. In contrast to the Dichograptidae, the mostly long nemacaulus is straight, stiff and fragile, as clearly evinced by the fact that, with the exception of the synrhabdosomes of Diplograptus found in New York, nothing but broken off rhabdosomes of these immensely common graptolites have been found. This character of the nemacaulus is incompatible with the assumption that these forms could have lived in the agitated waters near the surface of the ocean. For this reason they

must have lived either in quiet bottom waters, as Wiman has urged on account of this stiffness of the nemacaulus, or have been floating in somewhat deeper and quieter waters than the Axonolipa. The latter alternative presents, on account of the reversed direction of growth of the thecae, the most probable hypothesis. It is supported by other facts and considerations. The character of the central vesiclelike body in Diplograptus described before as pneumatophor by the present writer [1895], the presence of the rudderlike expansions of the distal ends of the rhabdosomes in several species and the bladelike form of the entire rhabdosomes of others, would suggest the adaptation of the synrhabdosomes to a vertical and oblique rising and sinking.

Among the Axonophora a strong tendency to a lightening of the rhabdosomes by extensive perforation of the peridermal walls, which finally leads to a perfect reticulation, makes itself felt, as well among probable descendants of the Diplograptidae as among those of the Climacograptidae, and leads to the production of the genera Retiolites, Stomatograptus, Gothograptus, Lasiograptus, Clathrograptus and Retiograptus. The purpose of this tendency can not be well understood, if either an attachment to seaweeds or to the bottom is assumed, since in either case only a weakening of the protective covering without apparent accruing advantage would be attained; but it is readily referred to a planktonic mode of existence, as all planktonic forms tend to lighten their shells.

It might be further mentioned that in certain beds of the Utica shale of the Mohawk valley fragments of seaweeds are by no means rare and are often covered with such organisms as the sessile Conularias, described by the writer, but that in no case have colonies of the axonophorous graptolites been found attached to them; the graptolites occurring in these beds are, on the contrary, only represented by detached rhabdosomes.

Another argument for the free planktonic mode of life of the Diplograptidae at least, is seen by the present writer in the observation published by him before [1895], that the siculae, discharged from the gonangia are already provided with their pneumatophors while in the Hydroidea, where

an exactly analogous growth stage is produced [p.523], the planula is discharged, which does not produce disk, hydrocaulus and first theca till after fixation. It is now inconceivable that these disks of the siculae of Diplograptus could have been intended as organs of attachment, as, wherever attachment of the embryo takes place the disk is formed only after attachment and as a result of it. As the Axonolipa had changed from pseudoplanktonic to holoplanktonic forms, it is to be inferred that the disks of the siculae originally were actually organs of attachment, but assumed secondarily the function of floats, and that then, by acceleration of development or retention and brooding of the embryos within the gonothecae, the disks, which originally formed only after contact of the embryos with foreign bodies, were produced within the gonangia.

It would finally appear that the change from a pseudoplanktonic mode of existence by attachment to seaweeds to a holoplanktonic mode would be easily accomplished by the accumulation of gas in some portion of the supporting organs. It would, for instance, be possible that a transudation of gas took place into the space between the principal layer of the perisarc and the epidermal layer of the primary disk, thus producing the tenuous "pneumatophor" described by the writer. Further, the vesiclelike expansions of the nemacaulus and of the distal appendages of certain species of Diplograptus, as D. physophora, vesiculosus and laxus [pl.16, fig.3] are plausibly explained as organs which assisted in floating the synrhabdosomes, and eventually protected the broken-off rhabdosomes from sinking.

### 7 Mode of reproduction and ontogeny

Early growth stages of graptolites are of very common occurrence in the graptolite beds. They, therefore, soon attracted the attention of observers; and Hall has figured [1865, pl.B] a number of such "germs" without, however, referring them to any definite species. He also recognized clearly that the growth of the rhabdosome begins with the minute spinelike

body which he termed the "initial point" or "radicle," and for which Lapworth later on introduced the term "sicula."

The details of the structure of the sicula have been elucidated by Wiman, who has demonstrated that it consists of two very different parts [*see* fig.2, 2a, 2b]. The initial part is a smooth[1], thin walled conical body that does not show any transversal growth lines and tapers at one end into a hollow tube, the nema, while the other, wider end is directly continuous with the apertural part of the sicula, which is the larger and thicker

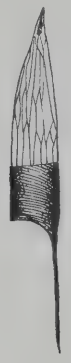

Fig. 2 Diplograptus sp. Sicula, showing the characters of the apical (embryonic) and apertural parts. From the Baltic sea limestone of Bornholm. x37 (Copy from Wiman)

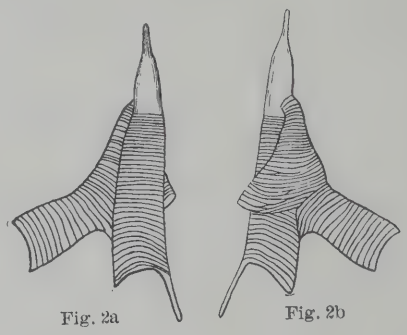

Fig. 2a Fig. 2b

Fig. 2a, 2b. Obverse and reverse views of the young rhabdosome of a dichograptid showing the sicula, its two parts and the gemmation of the first theca. From the Asaphus-limestone of Oeland. x27 (Copies from Wiman)

walled portion; is provided with growth lines and in form approaches a theca. The sicula has for this reason been termed the first theca by Holm.

The question appears pertinent, whether in the sicula itself (its apical part) we have to see a product of sexual reproduction or of some form of gemmation. This leads to the further inquiry after the *organ of reproduction* of the graptolites.

Hall believed he had found such organs in appendages of the rhabdosomes of Diplograptus whitfieldi [1859, p.507], which give the impression of macerated or ruptured vesicles. But no siculae were found in connection or inclosed in them; and a large series of specimens of

[1]In Diplograptus provided with longitudinal anastomosing thickenings.

such forms, collected by the writer some years ago in the Normanskill shale of Mt Moreno, as well as an inspection of Hall's types in the American Museum of Natural History, have convinced us that these apparent appendages are of the character of the peripheral fibrous tissues of Lasiograptus, as will be more fully shown in the second memoir on the *Graptolites of New York*. Frech [1897, p.551] has suggested that these appendages may have been "Deckstücke" (protective persons) or swimming bells (nectophores).

Nicholson saw gonangia in elliptic or orbicular chitinous bodies, for which he proposed the name Dawsoniae. These very common bodies have however never been found attached to graptolite rhabdosomes and form probably themselves an aberrant type of graptolites [Appendix, p.738].

Holm and Wiman have recognized the presence of small tubes in the Dendroidea which flank the thecae, and asserted the gonangial function of these. No sicula has been found in connection with these tubes, while distinct siculae occur in the Dendroidea, as for instance in Dictyonema flabelliforme [pl.1]. Frech considers these tubes homologous to the nematophores of the living Plumularidae.

Cysts, actually containing siculae, of two species of Diplograptus, have been described by the writer [1897]. [*See* text fig.9]. These were held to be gonangia or organs for sexual propagation. Wiman has expressed his dissenting belief that they ought rather to be considered individuals of asexual propagation or budding individuals [1895, p.73; 1896, p.192]. In support of my own conception I would cite the following arguments:

1 The homology in the structure and development of the sicula and the embryos of Hydroidea, as Eudendrium, which is discussed below [p.523]. The embryos of Eudendrium are, of course, of sexual origin.

2 Every rhabdosome begins its growth with a sicula. As new colonies among the recent Cnidaria and other colony-forming invertebrates take, with rare exception, their inception from sexually produced embryos, it is to be inferred that these extinct rhabdosomes also originated from such. It is

certain that there was intercalated in the multiplication of thecae and growth of the colonies by budding a sexual process of reproduction, and this would be most naturally expected to precede the inception of new colonies, or the formation of the siculae.

3 The cysts of Diplograptus, in which the siculae are produced, are comparable in structure and position to the gonangia or gonothecae of the calyptoblastic Hydroidea, i. e. to the external, chitinous receptacles of these living forms, in which either sporosacs or planoblasts are developed. Both the sporosacs and planoblasts are generative buds, with the difference that the sporosac remains inclosed within the gonangium, giving there origin to the generative elements — ova, or spermatozoa — while the planoblast is a generative bud which is fitted for a free locomotive life and becomes detached from the hydrosome. As the product discharged from the cysts of Diplograptus, the sicula, directly produces new colonies, it can not have been a free generative bud like the planoblast; and it is hence to be inferred that the generative elements of Diplograptus were produced within the gonangia, and that the ova directly ripened therein into siculae.

It is true that, in the propagation of Diplograptus by siculae, it has been found that a part of the siculae remains attached to the mother colony, growing out directly into new rhabdosomes, while others are discharged with the evident purpose of forming new colonies or synrhabdosomes. The former might be considered as suggesting, by the retention of their connection with the mother colony, an asexual origin or the nature of buds; but, then, it must be considered that the colonial stock or *synrhabdosome* of Diplograptus is actually a person of a still higher order than a common colonial stock of a hydroid, for it is a colony of colonies, as each "stipe," on account of its origin from a sicula, is homologous with the entire colonial stock, or *rhabdosome*, of a dichograptid or dendroid.

In the earlier forms, viz the Dendroidea and Graptoloidea Axonolipa, the reproduction may have been different, in so far as no siculiferous cysts have been found; and for this reason it is probable that the embryos were discharged at earlier stages. But the final product of the embryonic

development was also a sicula. In the Dendroidea it is possible that the flanking tubes of the thecae, considered by Holm and Wiman to be gonangia, contained the sexual products. In the Axonolipa nothing has been found as yet which would suggest receptacles for the development of the generative elements; for the entire rhabdosome is composed of nothing but thecae or supposed nourishing individuals.

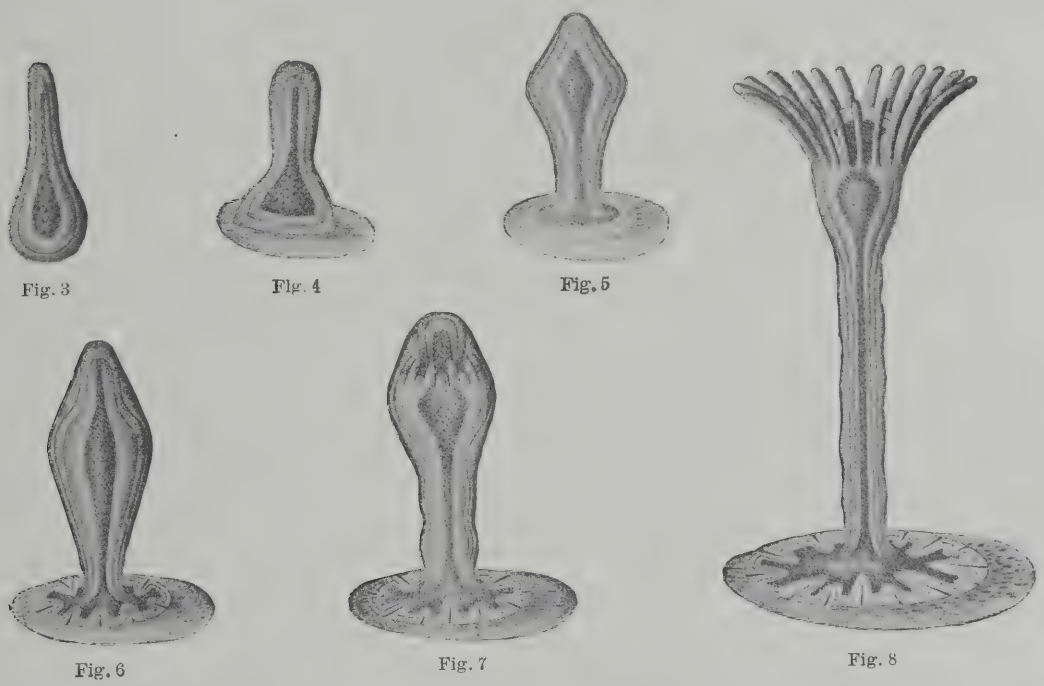

Fig. 3 Fig. 4 Fig. 5 Fig. 6 Fig. 7 Fig. 8

Fig. 3-8 Eudendrium ramosum Linn. Growth stages (Copy from Allman)

The initial part of the sicula is obviously to be considered as the embryo sheath, as also suggested by Holm.

The hollow nema is, as the writer's shale material shows, extended into a primary disk [pl.2]. The complete embryonic shell consists hence of a disk and a short cone, connected by a hollow tube. The question arises, then, whether one of these parts was formed before the other or whether all originated together. The answer to this problem is probably furnished by the development of certain hydroids, that pass through a growth stage

which is exactly alike in its structure and which hence can be considered as equivalent to that of the graptolites here under discussion. I copy here for comparison the successive stages of a tubularian hydroid, Eudendrium ramosum, from Allman [1872, pt2, pl.13, fig.12–16]. The similarity of the embryos in the graptolites and this hydroid is increased by the fact that the embryo of the latter produces a delicate chitinous sac.[1]

In figure 4 the planula has "become fixed by a disklike enlargement of one extremity."

In figure 5 "the disk of fixation has become more decidedly differentiated, while a delicate chitinous perisarc has become excreted over the whole surface of the embryo."

In figure 6 "the disk has begun to be divided into radiating lobes, and the hypostoma has become differentiated."

In figure 7 "the hydranth is now distinctly differentiated from the hydrocaulus, while the tentacles have begun to sprout round the hypostoma, and within a delicate chitinous sac, which envelops the whole."

In figure 8 "the hydranth has attained to nearly its ultimate form, and has burst through the chitinous sac, which has hitherto confined it, and the tentacles are now free to extend themselves in the surrounding waters."

There is no visible ground for the assumption that, inasmuch as the embryo of the graptolite shows the same composition of disk, nemacaulus and conical sheath, the formation of its embryonic sheath did not take place by the same processes of differentiation of an originally saclike covering into a disk and closed cone, and the gradual lengthening of the apical part of the cone into a nemacaulus.

After the bursting of the embryonic sac, the zooid began to grow and formed the apertural part of the sicula, the increment producing the transversal growth lines.

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[1]The presence of the chitinous covering of the embryo in the graptolites has repeatedly been cited as an important difference from the hydroids [p.576], but, as this instance shows, without propriety.

In the only case, where the organ containing the siculae has been observed, viz in Diplograptus foliaceus, it has been found that these originate in cysts, which surround the base of the whole synrhabdosome [p.528], and that they are partly retained, growing out into new rhabdosomes, and partly discharged, producing new synrhabdosomes. Here the young pass therefore apparently within vesicles through postembryonic stages, which in the Hydroidea are passed only after fixation of the embryo. This is evidently a secondary adaptation to the free planktonic mode of life of the Axonophora.

The fact that no such sicula-bearing vesicles have been found attached to any of the frequently observed rhabdosomes of the Dichograptidae would indicate that in these forms, which were pseudoplanktonic, the young were discharged already in their planula stage, and the subsequent growth stages were passed after attachment to foreign bodies, as in the living Hydroidea.

The sicula has been termed the first theca by Holm. While Wiman's investigations have taught us that the apertural part of the sicula, indeed, has the form and function of a theca, it can also be inferred from his work, that it still differs in essential characters from all later thecae of the same rhabdosome. Thus in Diplograptus there is formed a solid axis, the virgula, in the wall of the sicula, which is lacking in the other thecal walls, and the aperture is provided with a long spine (the distal extension of the axis) on one side, and with two lobes on the opposite. All of these characters fail to develop on the thecae. Elles's and Wood's and the writer's investigations have further demonstrated that the siculae frequently differ in their dimensions from the thecae of the same rhabdosome. It is therefore to be inferred that the first zooid, occupying the sicula, must have differed in essential characters from the later individuals produced by gemmation. It is, for this reason, appropriate to designate this first theca always by a special term, viz sicula.

The presence of a rod in one side of the sicular wall and that of the two lobes on the opposite side of the aperture gives to the sicula a particularly

conspicuous bilateral symmetry, as Wiman has pointed out [1893, p.269] This author lays great emphasis on this fact in the discussion of the possible relations of the graptolites to the Hydroidea, and we shall recur to this character in a later chapter [p.576].

Lapworth, as early as 1876, when describing two species of the new genus Dimorphograptus, expressed his belief that the sicula never develops more than one bud, even in the diprionidian forms. This view has been confirmed by Holm's, Wiman's and the writer's observations on representatives of different orders of the graptolites, and it can now be asserted that in all graptolites but one bud originates from the sicula.

With this the process of continuous budding is initiated, which results in the formation of the rhabdosomes.

Series of growth stages of colonies have thus far been published only by the present writer, viz those of the synrhabdosomes of Diplograptus foliaceous [1895] and of the rhabdosomes of Goniograptus thureaui [1902, p.576–93], to which is added in this publication a series of the growth stages of Dictyonema flabelliforme. It thus happens that these represent the three orders of graptolites, the last named graptolite giving an example of the development of the Dendroidea, Goniograptus thureaui of the axonolipous Graptoloidea, and Diplograptus foliaceus of the axonophorous Graptoloidea.

The *astogenetic series*[1] of Dictyonema flabelliforme is described in greater detail under that species. We shall, therefore, mention here but the principal facts. It begins with a distinct sicula, provided with a very long nema and a primary disk [pl.1, fig.1]. From the sicula buds first a

[1] We adopt here a recent suggestion by Dr E. R. Cumings [Development of Some Paleozoic Bryozoa. Am. Jour. Sci. 1904. 17:50], who submits a new set of terms for the growth stages of a colony in distinction to those introduced by Hyatt for the ages of an individual, and shall use here the term *astogenetic series* for these growth stages of a colony. In a former paper [1902, p.591], in which for the first time has been pointed out the recognition of stages in the development of a colony which correspond to the ontogenetic growth stages of an individual, we have employed the terms of the latter series in a wider sense.

single theca, which, however, as Wiman's sections of rhabdosomes of other species of Dictyonema would suggest, is probably of a composite nature and consists of a nourishing individual and a budding individual. It thus represents already a branch. This first branch diverges at an approximately right angle from the sicula. Several more buds of thecal appearance and apparently composite nature originate in succession, one from the other, all arranging themselves around and close to the sicula, thus producing a whorl of branches radiating from the apertural part of the sicula [pl.1, fig.13, 15]. These branches of the first order at once give origin by dichotomy to branches of a higher order, which continue the same process. Thus is produced the multitude of straight branches, which, growing downward and outward, arrange themselves on the surface of an imaginary bell.

With the *astogenetic development* of *a multiramous colony* of the *axonolipous Graptoloidea*, we have become acquainted by the material of Goniograptus thureaui from the Deep kill. The astogenetic series of this form has been described in the New York State Museum bulletin 52; and is more fully treated in this memoir under that species [p.621 and pl.6]. It represents a type of development different from that of Dictyonema flabelliforme in several features, while it can be said to be typical of the whole mass of Dichograptidae.

From the sicula a single theca buds, which is noncomposite and turns to one side in a horizontal direction. From this theca originates a second theca, which, falling into the same line with the first theca, turns in opposite direction. These first two thecae form the crossbar at the center of all the dichograptid rhabdosomes, which has been termed the "funicle" by Hall, and which hence is composed of thecae like the rest of the colony.

Both of the first two thecae divide again dichotomously, producing thus four branches of the second order, which repeat the same process, the result being eight branches of the third order.

After this stage is reached, in one half of the branches the thecae adopt a serial arrangement these becoming the "denticulate" branches of

the earlier authors, while the others continue to bifurcate, forming the so called stems. Both kinds of branches consist of thecae.

The early stages of all multiramous Dichograptidae are identical with those of Goniograptus.

A third series of *growth stages*, found in the New York rocks, is that of Diplograptus foliaceus. This again is representative of the *axonophorous Graptoloidea* and differs fundamentally from either of the two mentioned before. It has been fully described and figured in the *14th*

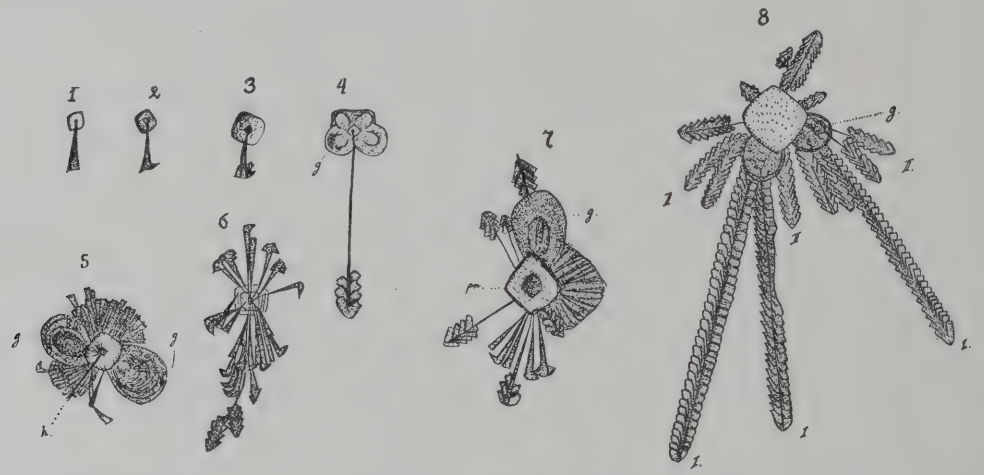

Fig. 9 (1-8) Diplograptus foliaceus McCoy. Series of growth stages. g, gonangium; *pn*, pneumatophor; I, first generation of rhabdosomes; II, second generation (Copy from Ruedemann)

*Annual Report of the New York State Geologist* [pl.3]. We copy here the drawings of some of the most characteristic stages. These show that the growth of the synrhabdosome of that diplograptid also begins with a sicula provided with nemacaulus and disk [*see* fig.9].

From the sicula originates again a single theca [*see* fig.9–2]. This, as Wiman has demonstrated [*see* fig.10] grows for a short distance downward in the direction of the sicula, but then turns abruptly aside and the next theca grows upward along the sicula in a proximal or antisicular direction and turns to the opposite side of the sicula. A continuation of this process of budding and alternate arranging of thecae produces the first stipe, which apparently consists of two separate series of thecae [*see* fig.9–4].

As the writer has pointed out in the paper mentioned, the thecae, and with them the entire rhabdosome, grow along the nemacaulus toward the central organs, hence in a direction directly opposite to that found in the typical Dichograptidae. The nemacaulus itself lengthens rapidly [*see* fig.9–4].

Before the primary rhabdosome has reached mature size, cysts appear around the base of the nemacaulus on the primary disk [*see* fig.9–4], which in older specimens are filled with siculae [*see* fig.9–5]. These cysts, which have been termed gonangia by the writer and considered vesicles, containing the products of sexual reproduction, open finally, a part of the siculae is discharged and form new separate rhabdosomes, while the others remain in contact with the primary disk and evolve in the same fashion as the primary rhabdosomes into new rhabdosomes [*see* fig.9–7], thus producing the radiating groups of rhabdosomes. Successive generations of gonangia produce whorls of rhabdosomes which differ in length, each whorl representing the rhabdosomes grown from a different generation of siculae [*see* fig.9–8].

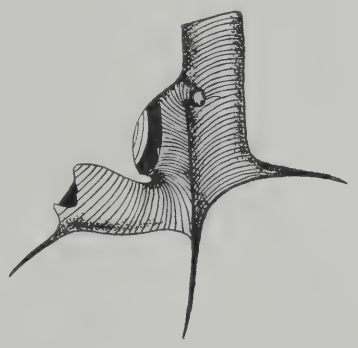

Fig. 10 Diplograptus sp. Apertural part of sicula and first theca, showing the perforation from which the second theca will grow. x37 (Copy from Wiman)

It will be noticed that the development of the rhabdosomes of the axonophorous Graptoloidea differs in the following facts from that of the axonolipous Graptoloidea. The nemacaulus of the sicula becomes, by the retrograde growth of the thecae, incorporated into the rhabdosome as a part of the axis, while in the Dendroidea and axonolipous Graptoloidea it remains free. The primary rhabdosome with its one stipe is homologous with the entire colony of the Dendroidea and axonolipous Graptoloidea, as it is produced by one sicula. As new rhabdosomes, each originating from a sicula, combine in Diplograptus into a composite colonial stock, this represents a rhabdosome colony or a person of a higher order than that of the Dendroidea and Dichograptidae, and the writer [*see* ch.4, p.483] has hence proposed for it the term synrhabdosome.

It has been pointed out by the writer in a former publication [1902, p.586ff] that not only did there exist in the graptolites ontogenetic growth stages in the development of the individual zooids, which, however, can not be traced in the fossils, but *the rhabdosomes in toto and their parts, the branches, seem also to pass through stages which suggest phylogenetically preceding forms.* These ontogenetic stages of the rhabdosomes express themselves in various ways, of which we select here the direction of the branches and the changing character of the thecae.

The original direction of the growth of the branches in the Dichograptidae has been in the approximate continuation of the sicula, i. e. an ascending erect position as long as the rhabdosomes were sessile on the ground. These became pendent [*see* ch.6, p.513] when the graptolites attached themselves in a suspended position to seaweeds, as numerous hydroids do today. To restore to the zooids their original, more advantageous, erect position, the branches began now to recurve, a process which in the Dichograptidae led to the Phyllograptidae, the horizontal, the reflexed, reclined and recumbent Tetragraptidae and Didymograptidae [*see* ch.10, p.543], and to the whole class of the Axonophora, where the thecae climb upward along the nemacaulus.

We find now in the majority of the Dichograptidae with the above cited growth directions of the branches, that the latter still retain their original dependent direction, in the proximal parts in some species, as in Tetragraptus fruticosus [pl.10, fig.1], Didymograptus nitidus, D. törnquisti and D. patulus, while in others, by the law of acceleration, the dependent proximal direction has already changed into a horizontal one, as in Tetragraptus serra, bigsbyi and taraxacum, the change in direction becoming progressively more abrupt as the final direction of the branches becomes reclined, as in T. bigsbyi, or recumbent, as in Phyllograptus.

In the Axonophora, where the growth direction of the rhabdosome has become entirely recumbent, it growing upward along the nemacaulus, only the first theca retains for a short distance the original downward direction, and then turns abruptly in a direction at right angles to the former. The

branches pass hence, in their development, through different directions representing ontogenetic stages that repeat stations in their phylogenetic development.

An analogous fact is found in the character of the thecae. The change which takes place in the character of the thecae within the colonies of the Dichograptidae has been described in detail in the paper noted before, on the development of Goniograptus thureaui [1902, p.586]. The writer has endeavored to demonstrate that in the rhabdosomes of that species two different kinds of thecae can be recognized, (1) those in the more proximal portions forming the bifurcating branches, for which the term *stolonal thecae* was proposed, and (2) those in the distal parts, notably in the serially arranged final branches. These were termed *brachial thecae*. The stolonal thecae are more cylindric than the brachial ones, remain narrower toward the aperture, less inclined to the axis of the branches and without any submucronate apertural processes.

A comparison of the form of the thecae of the younger dichograptid genera, as of Dichograptus, Tetragraptus and Didymograptus, with that of the older and presumably phylogenetically preceding genera, Bryograptus and Clonograptus, shows that in general the older genera have the more tubular, simpler thecae with less protected apertural margins. It is, hence, apparent that the stolonal or earlier thecae of the rhabdosomes represent indeed the older types of thecal form.

Observation of the thecae constituting the "denticulate" or final branches of Goniograptus thureaui, of Tetragraptus fruticosus [*see* fig.11], and of T. taraxacum has further brought out the fact that

Fig. 11 Tetragraptus fruticosus Hall. Branch which shows progressive change of thecae. x2½ (Copy from Ruedeman)

within these branches also a gradual change of the thecae from the stolonal or siculoid form to the brachial one takes place. In the species of Goniograptus cited, it has been shown that the earlier thecae of the branches have an inclination of but 7° as against 28° in the more distal, mature thecae, and overlap but one fourth of their length, whereas the later ones overlap more than one half and have straight apertures without marginal processes; these also have concave apertures with projecting, outer apertural margins.

It has been concluded from these facts that "the thecae of the colony of Goniograptus (and other Dichograptidae as well) from the sicula through the stolonal and early brachial thecae to the distal brachial thecae, form an ontogenetic series, which furnishes a clear and interesting example of localized stages of development," the existence of which has been demonstrated and their character elucidated by R. T. Jackson[1]. The principle of the localization of development expresses the fact that "in organisms that grow by a serial repetition of parts, it is found that there is often an ontogenesis of such parts which is more or less clearly parallel to the ontogenesis of the organism as a whole."

The asexually produced buds of the graptolites (thecae), like those of Hydrozoa and Actinozoa, are now to be considered as such localized stages. While they lack the stages seen in early embryonic development, they repass in general the later stages found in the ontogeny of sexually produced young.

The application of Jackson's principle to the colony of Goniograptus hence allows the conclusion "that the branches of the rhabdosome, like the leaves of a tree, indicate individually by their ontogeny the path along which they have been developed. The ontogeny of the branches demonstrates that the phylogenetically preceding forms possessed branches composed of more tubular thecae, with less overlap, looser arrangement, smaller deviation from the direction of the axis of the branch and straight, not mucronate apertures."

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[1] Bost. Soc. Nat. Hist. Memoir. 1899. v.5, no.4.

On the other hand, Didymograptus gracilis, a form with extremely long filiform thecae in the mature stage, possesses in its proximal part shorter, tubular thecae, of the Bryograptus type of thecal structure, thus indicating an opposite path of development to that observed in Goniograptus, but which also finds its expression in the ontogenetic development of the branch [*see* fig.12].

As noted before, the directions of the branches in the proximal parts present also an ontogenetic development, indicative of phylogenetic stages passed. Both the direction of the branches and the character of the thecae tend, hence, to support the same view, viz that the branches, though composed of thecae were connected into physiologic units.

Fig. 12 Didymograptus gracilis Törnquist. Enlargement of the specimen figured on plate 14, figure 17 to show more distinctly the sicula and the progressive lengthening of the thecae. Deep kill. x6

The writer has endeavored to demonstrate in the paper on Goniograptus that, not only the branches, but in fact the entire colonies of graptolites were organisms approaching closely to the character of individuals. One finds among the colonies all gradations from loose aggregates of individuals forming colonies to organisms in which, by division of labor, consequent suppression of individuality and the presence of common organs, the colony also morphologically approaches closely to the character of a sole individual, as in the Siphonophora.

The graptolite rhabdosomes now present, besides the ontogenetic characters of the proximal parts described above, various other features, which are suggestive of the physiologic individuality of the colonies. Some of these are the presence of a common float or pneumatophor, observed in several groups, and the geometric arrangement of the branches, which

became progressively more rigid and which served to maintain the equilibrium and to give to the greatest number of zooids the most advantageous position.

As, now, the graptolite rhabdosome so closely approached the character of an individual, and like such a one had its ontogeny and repassed ancestral stages, it is possible to recognize such ontogenetic stages of the whole rhabdosome and to apply to these the terminology introduced by Hyatt for the ontogenetic series of an individual. These stages have to some extent been traced in the rhabdosomes of Goniograptus with the following result[1]:

The embryonic stage is clearly present in the initial part of the sicula, which is differentiated from the distal part of the sicula by the nature of the periderm, which is thin, pellucid and possesses no growth lines. Holm asserts his belief that this initial, more pointed end of the sicula "corresponds to the original chitinous covering of the free zooid germ or embryo." It holds a position similar to the protoconch of the cephalopod shell. The nepionic or infantile stage is represented by forms [pl.7, fig.1–6] in which the successive dichotomous divisions produce the stems. It begins with the formation of the apertural part of the sicula. The neanic or adolescent stage of the colony begins with the formation of the branches with serial arrangement of thecae and ends, in the Goniograptus material from the Deep kill, with the production of six such branches on each of the four stems. After this, in the ephebic or mature stage, the branches continue to grow out to full length. The gerontic or senile age is marked by a thickening of the stems.

### 8 Structure and morphology

As much of the structure and morphology of the graptolites has been anticipated in preceding chapters, and more details are given in the generic descriptions, but a cursory statement of the principal facts regarding

[1] As we have before noted, Professor Cumings has meanwhile proposed to designate the growth stages of colonies by the prefix "asto."

those groups of graptolites which are treated in this memoir is needed in this place.

All graptolites are colonies of hydroid-like appearance. Only the carbonaceous (chitinous) periderm is preserved.

Probably all colonies originated from an embryonal zooid (sicula) and consisted, where complete, of (1) the organs of attachment, or suspension, (2) the supporting stems, (3) the thecae, and (4) the reproductive organs.

The organ of attachment may be a part of the first embryonal zooid (primary disk) or a secondary disk (central disk) or a rootlike expansion. The first organ is probably found in the young stages of all graptolites, and in the mature stage of all smaller Axonolipa and probably in all Axonophora; the second in some larger forms of the Dichograptidae (genera Tetragraptus and Dichograptus). Perhaps it occurs also in some species of Didymograptus, as in D. patulus. The rootlike expansions have been observed only in some Dendroidea (*see* Dictyonema).[1]

Between the sicula and the primary disk is intercalated either a thin, often very long, filament, the nema, in the young of some Dendroidea (Dictyonema flabelliforme) and the Axonolipa, or a more rigid, narrow tube (nemacaulus) in the Axonophora, which in the latter is (always?) supported by a strengthening rod (virgula)[2] originating in the wall of the sicula.

From the sicula originates the first theca, and by continued gemmation of thecae the branches are formed. The second theca in nearly all Grapto-

[1] In some Axonophora a vesicle has been found by the writer to surmount the primary disk. This is considered to have had the function of a pneumatophor.

[2] The inclosure of the virgula within the nemacaulus of the Diplograptidae can be inferred from an observation made by the writer [1895], who found in a flexed specimen, that the virgula had separated from the nemacaulus [*loc. cit.* pl.2, fig.6]. The latter is, according to Wiman, who observed its initial part, a hollow tube. Sometimes the nemacaulus becomes inflated into a vesicle, as in Dipl. appendiculatus (Törnq. ms.) Elles *emend.* Inside this vesicle the virgula can, according to Elles [1898] be quite well detected; and it is also figured [*ibid.* fig. 30] by that authoress as a straight rod extending through the vesicle.

loidea (with the exception of unbranched forms, as Azygograptus) crosses over and places itself on the opposite side of the sicula. This often prominent proximal part of the second theca, which in the multiramous forms connects the common canals of the first four branches, has been termed connecting canal by Holm, but this term was applied by Törnquist to the first part of the first theca. Elles and Wood call it the "crossing canal."

In the Dendroidea the branches consist of three different kinds of tubes: large thecae, which are supposed to have contained nourishing individuals, smaller tubes, which are budding individuals, and from which all three kinds of tubes originate, and longer, narrow tubes (gonangia, after Holm and Wiman; nematophores, according to Frech). For further details see under Dictyonema and Dendrograptus.

In the Graptoloidea only thecae of one kind are observable which contained nourishing zooids. These exhibit in some compound Dichograptidae (Goniograptus, Tetragraptus) certain differences proceeding from the base of the colony in a distal direction, which are of an ontogenetic character [*see* ch.7, p.531]. The apertures of the thecae are often provided with one or several mucros or spines. These and other characters give to the theca a bilateral symmetry. The external and internal apertures of the thecae are in most or perhaps all Graptoloidea provided with a ringlike thickening [*see* Perner, text fig.1, 2, and Didymograptus bifidus, p.692, of this publication].

In the axonolipous Graptoloidea the thecae grow in a distal direction and are connected and held by their bases only, which form a continuous canal (common canal). In the Axonophora the first theca assumes, after a short distal growth, a reverse direction, which is followed by all succeeding thecae. These attach themselves to the nemacaulus. The latter is here supported by an independently formed axis (virgula).

It appears that also in the heavier branches of the Axonolipa, as in Tetragraptus amii [*see* pl.11, fig.1] a support of the branches was obtained by a thickening of the dorsal wall (common canal) of the branches.

The *branching of the rhabdosomes* takes place in different ways. In

Dictyonema, according to Wiman, a generation preparative to a branching produces a theca and two budding individuals instead of a theca, a budding individual and a gonangium. Each of the budding individuals then produces the three kinds of individuals; the resulting two groups of individuals forming with one or more of the old thecae, the new branches, which are thus of perfectly dichotomous origin. In the forms referred by the same author to Dendrograptus the process is essentially the same. In Inocaulis one has to differentiate between branches and branchlets or twigs. Each of the latter consists of four individuals, two thecae and two gonangia, which originate in the branches and open on the twigs. In Callograptus the mode of the formation of branches is not yet known.

In the axonolipous Graptoloidea branching is accomplished by two successive thecae, which turn to different sides and thus become the mother thecae of new branches. In the early axonophorous Graptoloidea, described in this publication, no branching takes place within the rhabdosomes or persons of the second order.

The arrangement of the branches varies greatly in the Dendroidea; the branches are distributed irregularly in treelike fashion in Dendrograptus, arranged into a funnel or bell-shaped rhabdosome in Dictyonema, into a similar or probably flabellate form in Callograptus, while in Ptilograptus the irregularly arranged branches are plumose, the branchlets rising alternately on opposite sides of the branches.

In the axonolipous Graptoloidea the earliest genera, Clonograptus and Bryograptus, possess an irregular arrangement of the branches. From these two develop, by a progressive reduction in the number of branches, forms with a regular disposition of the branches, namely the genera Loganograptus, Dichograptus, Tetragraptus, Didymograptus and Phyllograptus, forming one group, the genera Sigmagraptus, Coenograptus, Pterograptus and Pleurograptus another, and the genera Temnograptus, Schizograptus, Ctenograptus, Holograptus, Rouvilligraptus and Trochograptus, a third.

In the first group only dichotomous branching is observed, in the others the dichotomous and monopodial modes of branching form various combina-

tions. While the two modes of branching produce very different appearances of rhabdosomes, there exists probably no essential difference between them. In one case the mother theca produces a daughter theca, so early that it has not progressed sufficiently to force the latter into a new direction, but both assume new directions, while in the monopodial branching the mother theca has already established its direction, that of the preceding branch, when it sends out a daughter theca, which then alone diverges from the old direction.

Within the Dichograptidae the angle of divergence changes within the whole compass of the circle, a complete reversion in the direction of the branches gradually taking place. This fact will be noted more fully in the chapter on the classification and phylogeny of the graptolites.

The structure of the rhabdosomes of the graptolites with diprionid arrangement of the thecae, such as the Diplograptidae and Climacograptidae have, has been little understood till recent years, but it is now known that, as a rule, and notably in Diplograptus, the rhabdosome is composed of thecae which have assumed a proximal or centripetal direction of growth along the nemacaulus of the sicula, whereby each theca buds from the opposite side of the adjacent more distal one, all arranging themselves thus in two series but actually belonging to one. In certain forms, as in Climacograptus kuckersianus [Wiman, 1888, p.190], one of the thecae (the third in the species cited) sends out two thecae, and thus two separate series originate which are divided by a longitudinal septum.

In the Monograptidae which have been derived from the Diplograptidae and Climacograptidae, only one of these series is developed, but the thecae retain their centripetal growth.

While in the Diplograptidae the tubular thecae have an oblique position to the principal axis of the rhabdosome, thus producing the dentate appearance of the latter, they have a rectangular form in Climacograptus and its derivatives, and are appressed in a position parallel to the axis, whereby their outer margins form lines parallel to the axis which are interrupted by the transversal notches of the apertures.

In some genera of both series, the Diplograptidae and Climacograptidae, the peridermal walls of the thecae may become dissolved into a system of meshes. In the genus Retiograptus, which is, in the faunas here described, represented by one species, this dissolution is incomplete, and the meshes appear only along the apertural margins. This genus appears also to stand apart from the other Axonophora by the vertical position of the thecae on the axis. Owing to its being known only from shale material it is, however, but little understood, and its characters need further elucidation.

The same can be said of the genus Trigonograptus, to which a characteristic species of the zone with Dipl. dentatus has been referred. The most striking and apparently sole differential character of this genus is the lack of any interruption of the outer margin by apertures. This is, as our material shows [pl.17], produced by the peculiar position of the apertures, which lie so oblique to the axis of the thecae that they are subparallel to the principal axis of the rhabdosome.

Certain Diplograptidae are characterized by long apertural spines. These attain their extreme development in the species referred to Glossograptus.

In the Dendroidea and axonolipous Graptoloidea only persons of the first order (thecae) and of the second order (rhabdosomes) have been observed; in some of the Axonophora, however, (Diplograptus, Retiograptus) it has been found that the rhabdosomes, each of which originates from a sicula, combine into a colony which is thus a person of the third order.

On receptacles for organs of sexual reproduction, see chapter on mode of reproduction, page 519.

### 9 Histology and chemical composition of the periderm

Richter [1871] was the first to call attention to the structure of the periderm. He discerned two layers, an exterior, very flexible one, which is again composed of two thin lamellae, and a thicker internal one, which is provided with transversal ridges.

Gümbel treated, a few years later, polished specimens with acids and came to a like conclusion with Richter. He also inferred that the

periderm had originally consisted of the same chitinous substance as that of the sertularians.

In 1893 Sollas published some notes on the peridermal layers of Monograptus, giving their dimensions.

Perner used specimens of Monograptus and Retiolites embedded in limestone to prepare his sections. By means of these he was enabled to discern four different layers, namely (1) the epidermis (*couche épidermique*), which appears as a fine, brown line, (2) the black layer (*couche noire*), a thick, black, supposedly chitinous band, (3) the angular layer (*couche à coins*), the thickest layer, which is brown and marked by angular or zigzag lines, (4) the columnar layer (*couche à colonnettes*), a thin, brown layer, consisting of small columns and possessing a darker layer, suggesting an internal epidermis.

Wiman [1895, p.39] was unable to discern anything more than the black layers in sections of Monograptus, made from Swedish material, but he observed the external epidermis and the black layer in sections of Dendrograptus and the external and internal epidermis and the black layer in sections of Monograptus priodon from Perner's locality. In decolorized specimens of Diplograptus he was also able to discern the black layer with its growth lines and the superjacent epidermis in continuous patches.

Gürich [1896] has revised Perner's observations on the periderm of Monograptus and found that the angular layer (*couche à coins*) consists of calcite crystals and is secondarily formed during fossilization; and that the brown layers observable outside and inside of the black layer are zones of pigment which either are derived from the black layer or formed a superficial layer of the same. The epidermis and columnar layers have not been observed by Gürich.

A layer of graptolite bed 2 (Tetragraptus zone) at the Deep kill, in which the graptolites are retained uncompressed in pyrite, provided the present writer with material for thin sections, principally specimens of Phyllograptus ilicifolius and branching dichograptids. In these the walls consist uniformly of three layers, viz the black layer, the angular

layer and the columnar layer [*see* fig. 13, 14]. The last two are distinctly composed of calcite crystals. As these two zones are correlatives in their width — the one is in some places entirely replaced by the other — and as they are separated by a jagged line, corresponding to the sections of crystals, it is to be inferred that they result from a single deposit of fibrous calcite crystals, which, being slightly curved, show in the angular zone their sections and in the columnar zone their lateral faces. Bands of brown pigment appear at irregular intervals in the angular zone. No traces

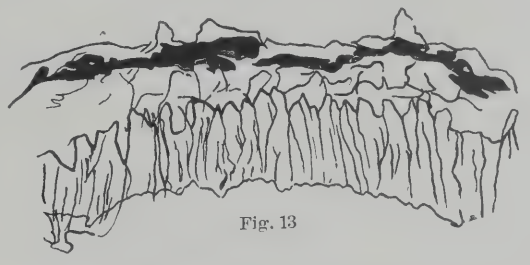

Fig. 13

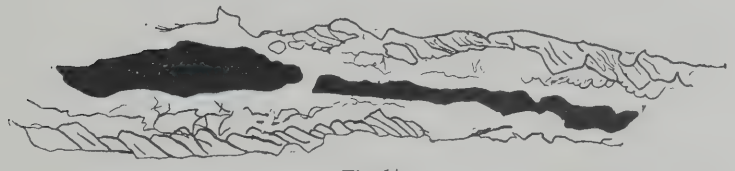

Fig. 14

Fig. 13, 14 Dichograptus sp. Thin sections through walls of pyritized specimens. Deep kill. x215

of an exterior or interior epidermis have been observed in any of the sections, but it is quite possible that these, if present, are, on account of their thinness, entirely concealed by the pyrite matrix.

It can be considered however as established by Perner's and Wiman's observations that there existed an "epidermis" besides the principal black wall. In other forms, as in numerous species of Lasiograptus, which the writer has collected in the Trenton graptolite beds, and which will be described in the next memoir, the thin epidermal layer and the principal one, which there is dissolved into a network of fibers, can be readily discerned.

The angular and columnar layers can not be considered layers of the periderm of the graptolites, though they may correspond to some part of

the living animal, no longer determinable, as is pointed out by Frech [*loc. cit.* p.551]. In reference to this last suggestion, it is however to be remembered that the calcite layer, though of remarkably uniform thickness, is not always found on the same side of the carbonaceous periderm and, though mainly developed on the inside, may also occur on the outside or even on both sides [*see* fig.14]; and that, further, the calcite band is often directly continuous with the numerous small calcite veins transecting the pyrite. The latter fact would suggest that the calcite band may have been formed after the hardening of the organic material which caused the deposition of the pyrite. That the latter filled the rhabdosomes at a very early stage of the fossilization, is attested by the failure of these rhabdosomes to become compressed. On the whole, the calcite bands in the Deep kill material appear to have filled the interspaces between the periderm and the organic or pyrite matrix, arising from a shrinkage of the latter.

The presence of an epidermic layer which, according to Wiman's observations, appears to have had its independent system of growth lines, seems important in so far as it would indicate that the periderm was not an external skeleton, but was formed in the mesoderm. The latter conclusion has urged itself on the writer ever since he studied the colonies of Diplograptus, by various arguments, the most important of which are the following:

1 The nema or nemacaulus of Diplograptus pristis Hall (foliaceous Murchison) shows from the sicula onward to the perfection of the first or primary rhabdosome [*see* Ruedemann, 1895, pl.3, fig.8–14] a continuous growth in length and thickness, which in a horny, nonporous body can be explained only by the action of an external tissue. The secondary growth of the nema is also specially remarkable in Tetragraptus fruticosus [pl.10, fig.7].

2 The stems of the larger multiramous dichograptids, as notably Goniograptus [pl.6], which consist of thecae, continue to grow in thickness till almost all traces of their thecal structure have disappeared.

3 Certain species of dichograptids develop a secondary disk at the basis of the rhabdosome [*see* Dichograptus octobrachiatus, pl.8, fig.4].

This disk is not present in young individuals and continues later on to grow in correspondence to the size of the whole colony. Its formation presupposes an enveloping tissue.

4 There appear secondary spines and other appendages, mostly at the distal end, as in Climacograptus bicornis, which, lying outside of the thecae, attain a greater size and development than the individuals supposed to have lived in the small thecae, could have given them by their action.

5 There is found in some forms, as in Lasiograptus, an external framework consisting of horny filaments, which would suggest that it served to protect this soft covering tissue.

Finally we mention, that it has been claimed by Gümbel that the periderm consisted originally of chitin, though tests recorded by Wiman showed that no reaction, characteristic of chitin, is any longer obtainable from the fossils; that it can not be doubted that it once consisted of some chitinlike substance; and, further, that the periderm possessed a certain degree of elastic flexibility, for the nemas and rhabdosomes are frequently found bent and twisted without having been broken.

## 10 Classification and phylogeny of the graptolites

*a* **Review of classifications.** As the systematic arrangement of the organisms is to express their true relationship, it is evident that no arrangement can find general acceptance so long as the investigations on the morphologic and phylogenetic relations of a group of forms have not passed beyond their inceptive stages. This fact impresses itself at once on the paleontologist who attempts to find a generally adopted system for the classification of a graptolite fauna under investigation; for he will soon observe that not only the larger divisions which suggested themselves so readily, but also many of the genera which once appeared so well defined and compact, have lately lost and are still losing in value as natural groups.

It was natural that a grouping of the graptolites began with a separation from the graptolites proper of the arborescent forms grouping them-

selves around Dendrograptus and Dictyonema, which previously were only with some doubt united with the graptolites; and, further, that among the latter the forms with one series of thecae were opposed to those with two or more series of thecae. The arborescent forms were separated as *Cladophora* (Hopkinson) — now currently designated Dendroidea (Nicholson) — from the *Rhabdophora*, a term proposed by Allman under the wrong supposition that all graptolites proper had a strengthening rod, the virgula.

The number of series of thecae was first used systematically for the erection of several divisions by Hopkinson, who proposed the groups *Monoprionidae*, *Mono-Diprionidae*, *Diprionidae* and *Tetraprionidae*. Hopkinson's suggestions have been further elaborated in Lapworth's complete system (1873). In this the Rhabdophora are divided into two sections, viz (1) *Graptolitidae* and (2) *Retioloidea*. The Graptolitidae are characterized as developing the rhabdosome from a true sicula; having a coenosarc, from which originates a single series of thecae only (the Diprionidae included in this section were considered by Hall and others as possessing a "dibrachiate monoprionidian polypary, whose branches coalesce by the whole of their dorsal surfaces") and as having a dorsal virgula embedded in a narrow groove on the exterior surface of the periderm. The Retioloidea, on the other hand, were stated to have their rhabdosome never developed from a siculiform "germ," as having a coenosarc originating a double series of thecae, and as possessing an epiderm which is more or less supported by a framework of chitinous filaments.

The first section was further divided into (1) *Monoprionidae*, comprising the families *Monograptidae*, *Nemagraptidae* (Leptograptus, Amphigraptus, Pleurograptus, Nemagraptus, Coenograptus), *Dichograptidae* (Didymograptus, Tetragraptus, Dichograptus, Loganograptus, Clonograptus and four unnamed genera, represented respectively by Gr. multifasciatus, milesi, vagans and richardsoni); (2) the *Mono-Diprionidae*, comprising the family *Dicranograptidae*, with the genera Dicellograptus and Dicranograptus; (3) the *Diprionidae*, comprising the family *Diplograptidae* (genera Climaco-

graptus and Diplograptus); (4) the *Tetraprionidae* with the *Phyllograptidae* and the single genus Phyllograptus.

The *Retioloidea* were divided into the *Glossograptidae* (a provisional family with the genera Glossograptus, Retiograptus and Lasiograptus) and the *Retiolitidae* with the genera Clathrograptus, an unnamed genus for Retiograptus eucharis Hall, Trigonograptus and Retiolites.

This classification, which was supported by concise and clear generic definitions, given in an analytic table, has been generally adopted and has, as far as the grouping of the genera into families is concerned, thus far well stood the test of later investigations, so that, on the whole, the families appear to represent natural divisions. Lapworth himself claimed already for the families of the Monoprionidae that they represent natural divisions, seeing a confirmation of his claim in "the known geological distribution of the genera constituting the several families."

The investigations of Swedish paleontologists, on uncompressed material, have however demonstrated that some of the larger divisions contain heterogeneous material and that the forms constituting others are not entitled to comprise a group of higher rank. The Monoprionidae contain at least two widely different groups, viz the Monograptidae and the Dichograptidae. The former, which are among the last appearing Graptolitidae, have in their rhabdosomes proximally or inwardly directed thecae and a virgula, and are derivatives of the Diplograptidae; while the Dichograptidae, which contain some of the earliest genera, as Clonograptus, have distally directed thecae and lack a supporting rod within the branches. The division Monoprionidae is hence best discarded and has in fact not been used in the latest systematic arrangements, as those of Wiman and Frech.

The suborder Diprionidae has likewise become untenable on account of the fact that the rhabdosomes of the Diplograptidae are monoprionidian in origin, i. e. originate from one theca, the consequent close relationship with the Monograptidae, and the further fact that the Retioloidea contain forms with a like arrangement and origin of the thecae.

The Tetraprionidae (Phyllograptus) have been shown to be only an aberrant branch of the Dichograptidae in which the four recumbent branches coalesce.

Wiman has, in his paper "Ueber die Graptoliten" [p.25ff] applied the results of his researches to an improvement of Lapworth's system. He divides the graptolites into three groups, viz *Graptoloidea* Lapworth, *Retioloidea* Lapworth and *Dendroidea* Nicholson. Under these are arranged the families and genera, which are largely taken from Lapworth's "Improved Classification of the Rhabdophora." In this way he has placed later erected genera in their respective places, adding however, that in his belief many of them, notably among the Dichograptidae, are not deserving of generic rank.

A greatly differing system has been proposed by Frech [1897, p.568ff]. This author has, in recognition of the important fact, that all the later graptolites have a virgula incorporated into the rhabdosomes and bear the sicula at the distal end of the rhabdosomes, divided all graptolites into two orders, viz the *Axonolipa*, or forms without an axis, and the *Axonophora*, or forms with an axis. The Axonolipa contain the families *Dendrograptidi* (Dictyonema, Dendrograptus etc.) and *Dichograptidi* (including Dichograptidae Lapw., Leptograptidae Lapw., Didymograptidae auct. and Phyllograptidae Lapw.). The latter are again divided into the subfamilies *Didymograptini*, *Tetragraptini* and *Phyllograptini*. The Axonophora are subdivided into the families *Climacograptidi*, *Diplograptidi*, *Monograptidi* and *Retiolitidi*. The Climacograptidi, hitherto united with the Diplograptidi, are separated on account of the rectangular fixation of the thecae and the location of the apertures. This family comprises the genera Retiograptus, Climacograptus, Dicranograptus, Dicellograptus and Monoclimacis. It will be noticed that Frech unites here, by the direction and shape of the thecae, forms of very different appearance, as the biserial Climacograptus and uniserial Monoclimacis and transfers the genus Retiograptus, hitherto united with the Retioloidea, but in which the latticed sculpture of the periderm is still little developed, to the Climacograptidi. The family Diplograptidi has

been made the receptacle of the genera Diplograptus, Glossograptus and Dimorphograptus. The family Monograptidi has the same compass as is given to it by Lapworth. The Retiolitidae comprise the genera Retiolites, Gothograptus, Lasiograptus and Clathrograptus.

We have here adopted with some modification [p.570] Frech's terms Axonolipa and Axonophora, for the reason that they appear to give proper significance to important differences in the structure of the rhabdosomes. In the former the nema remains free and the thecae are directed distally; in the latter the virgula and nema become the axis of the rhabdosome and the thecae are directed proximally or centrally; in the former only single rhabdosomes have been observed, while in the latter, as far as complete material has been found, the rhabdosomes were united into synrhabdosomes, and thus a higher and more complicated form of colony attained. As the two orders are also separated in time, the Axonophora replacing the Axonolipa from the middle of the Lower Siluric formation onward, it can hardly be doubted that we have to see in these orders natural divisions of great import.

The fact that the Phyllograptidae among the Dichograptidae approach by the coalescence of their recumbent branches the Diplograptidae in external appearance, and that, also, the nema appears to become incorporated [*see* Phyllograptus anna mut. pygmaeus, p.716] into the rhabdosome as an axis, thus making this form axonophorous to some extent, is liable to lead to the misconception that this family contains forms with some of the distinctive characters of the Axonophora; but the four series of thecae in Phyllograptus represent separate coalescent branches, while in Diplograptus the two series are produced by the alternate arrangement of the thecae of but one series. The axis of the Diplograptidae is the virgula which is already formed in the wall of the sicula, while that of Phyllograptus anna mut. pygmaea is only the nema or supporting thread of the sicula. The axis of the Diplograptidae is hence a new acquisition not found in the Dichograptidae. In some Phyllograptidae, moreover, this thread has been lost or is, as Holm's observations on Phyllo-

graptus angustifolius indicate, no longer distinguishable within the coalesced dorsal walls of the branches.

*b* **Phylogeny of the orders of graptolites.** A problem not yet solved is the *relation of the Dendroidea to the Graptoloidea.* Frech considers the Dendrograptidi a part of the Axonolipa. In fact, they lack the supporting rod of the Axonophora, and their thecae are directed distally, while the sicula holds a proximal position. But they differ so greatly, not only in general appearance of the mature colonies, but also in the composition of the branches, from all other graptolites, that the question is pertinent, whether they should not be considered a separate order for themselves, specially as they also continue to coexist with, or rather persist beyond, all other graptolites.

It is here, however, not to be forgotten that several authors have recently been not disinclined to consider the Graptoloidea as derived from the Dendroidea. Thus Wiman [1893, p.35] has pointed out that a fragment of a dendroid is often externally undistinguishable from a fragment of a graptoloid, and suggested that the rhabdosomes of Graptoloidea may be but the external periderm of those of Dendroidea, and that in the former the delicate tubes (his "gonangia" and "budding individuals") filling the common canal of the Dendroidea, which also in these are rarely retained, may have been so thin walled that they never, or only in most exceptional cases, left any traces of their former existence. He adduces in this connection an observation of Hopkinson [1882, p.56], who observed in Tetragraptus serra and Didymograptus extensus, partitions between the proximal parts of the thecae and the common canal, which separate the latter by transverse septa into spaces corresponding to the thecae. No traces of these partition walls have been found by the writer in sections of pyritized specimens of several Dichograptidae, and it seems possible that the appearance of the partitions has been produced by cutting through the proximal parts of the thecae in somewhat obliquely embedded material. However this may be, it is to be conceded that the failure to observe the delicate tubes within the Graptoloidea, with the restricted number of observa-

tions of the internal structure of Graptoloidea, can not be considered as constituting a fundamental difference between the two orders.

Elles [1898, p.536] also places, in a table giving the "suggested phylogeny of a part of the Skiddaw slate graptolites," Dictyonema at the base of the system leading through Bryograptus to Tetragraptus and Didymograptus.

If we add that the sudden appearance of the progenitors of the Dichograptidae, the genera Bryograptus and Clonograptus, in the wake of the equally sudden and widespread appearance of Dictyonema flabelliforme may be due, as Lapworth has suggested, to the change of these forms from a sessile benthonic mode of life to a planktonic or pseudoplanktonic one, the conclusion appears legitimate that the Dendroidea precede the Graptoloidea in time, and that the possible transitional forms between the two orders, being still benthonic, are not readily accessible to observation; that, hence, the failure to observe them is no argument against their former existence.

It may be further stated that the possession of like initial receptacles, the siculae, and the similarity of the early parts of the rhabdosomes in Dictyonema flabelliforme and Staurograptus [pl.2] can also be regarded as suggesting common ancestors for these, and a consequent closer relationship, as the mature colonies would indicate.

As an alternative theory, the possibility of a derivation of the Dendroidea from the Graptoloidea has been pointed out by Wiman; this phylogenetic relation being considered by that author the more probable on the ground that differentiation of individuals frequently is produced by a division of labor. This theory, it is thought, might also explain the fact that the proximal thecae of Dictyonema peltatum are similar to those of Graptoloidea.

The solution to the entire problem of the relations between Dendroidea and Graptoloidea rests obviously with the discovery of earlier Cambric graptolites, and specially with that of the structure of the reproductive individuals in the Dichograptidae.

The connection between the Axonolipa and Axonophora is still obscure. The fact is that, where in the Lower Silurić the axonophorous genera appear — in the Mt Moreno beds and the Deep kill section in the zone with Diplograptus dentatus, with the genera Diplograptus, Climacograptus, Glossograptus, Trigonograptus and Retiolites — they at once come on the field in great force, and that the Axonolipa then rapidly disappear. Further, no form is known in the preceding zones which could be conclusively held to announce or foreshadow this new departure in graptolitic structure. We have here, hence, apparently an interesting illustration of the principle emphasized by Hyatt: that types are evolved more quickly near the point of origin, and that there are greater structural differences between genetic groups of the same stock while still near this point than appear subsequently.

The genera Diplograptus, Climacograptus, Trigonograptus and Retiolites, appearing suddenly side by side, encompass already the full amplitude of the structural differences as expressed in the position of the thecae found among the diprionid Axonophora; while Retiolites already indicates the perforation of the peridermal wall, that becomes fully developed in later phases, and Glossograptus already presents the extreme growth of spinous appendages in this class of graptolites.

It is known that a strong tendency to the perfection of the structure attained by the Diplograptidae and which insures a stable upward growth of the thecae, has manifested itself distinctly in the preceding Dichograptidae by the assumption of a reclined position of the branches and led to the development of such forms as the Phyllograptidae, the reclined Tetragraptidae (Tetragraptus similis) and Didymograptidae, as Didymograptus caduceus (gibberulus). It would hence seem proper to look among these reclined forms for the ancestors of the Diplograptidae.

An interesting observation, probably suggestive of the path of derivation of Diplograptus from the Dichograptidae, has been recorded by Törnquist [1901, p.23] and verified by Elles and Wood [1901, p.53]. The latter authors state of Didymograptus gibberulus: "The crossing canal is clearly seen just below the apex of the sicula, and rather above the initial

parts of the thecae which have developed later. There appears also to be a crossing canal (or something of a similar nature) between th. $2^1$ and th. $1^2$. Thus, as Törnquist points out [*loc. cit.*] 'The first stipe crosses the sicula and the second stipe the first theca.' This seems to show that in this species there is a deviation from the normal Didymograptus type of development, that is to say, a forecast of the type characteristic of the Diplograptidae."

If, indeed, the budding of thecae on alternate sides, which produces the double intertwined series of thecae in Diplograptus, originated with the first thecae of a Didymograptus with reclined branches, such as D. gibberulus, the acceleration of the development of the ancestral characters must have been extremely rapid, for the only vestige left of the former downward direction of the first thecae of the ancestral Dichograptidae is the short, initial, downward course of the first theca in Diplograptus and Climacograptus [text fig.10]. This and the downward direction of the sicula seem indeed to be the only facts of ontogenetic importance for a phylogenetic linking of the Axonophora with preceding graptolites. The fact of the replacement in time of the Dichograptidae by the Axonophora would seem to lend support to the assumption of this phylogenetic connection of the two orders of graptolites.

On the other hand, it should not be forgotten that the siculate rhabdosomes of the Axonophora unite into individuals of a higher order, the synrhabdosomes of Diplograptus and Retiolites, and thus an additional distinctive character is found in the Axonophora no indication of which is as yet known among the Dichograptidae.

The incorporation of the nemacaulus in the rhabdosome of the Diplograptidae as support of the backward or upward growing thecae, which, so to say, climb upward along the nemacaulus, has induced the formation of a special organ among the Axonophora, the virgula, which is found to originate within the wall of the sicula of these forms, as far as they have been studied. This appears, then, to be an interesting case of the transference by tachygenesis of a character, the virgula, newly acquired by a colony, to the embryonic stage (sicula) of the whole colony. The appearance of

this coenogenetic character in the sicula is also evidence of the extreme rapidity of development among the graptolites, evinced already by the rapid changing of the faunas in the successive beds.

It is, however, in my opinion, doubtful whether the solid axis or virgula of the Axonophora is a homologous organ in the different groups of that order. It seems almost impossible that the virgula of Diplograptus, which originates in the sicula and nemacaulus, and with the latter becomes incorporated in the rhabdosome, should be homologous to the bipartite axis found within the two reclined branches of Dicellograptus; for the nema from which the sicula of the latter was originally suspended, is, according to my observation and knowledge, never incorporated in either of the branches. The axes of Dicellograptus appear to be, for this reason, only thickenings of the dorsal wall of the coenosarcal canal, induced by the upward growth of the branches, while the virgula of the typical Axonophora is a separate rod. Such secondary strengthening of the branches is described in this memoir even from a dichograptid, viz Tetragraptus amii [p.647 and pl.11].

The early appearance of a Dicellograptus, viz D. moffatensis, in the zone with Diplograptus dentatus of the Upper Skiddaw slates, is very suggestive of the derivation of that genus, not from the later Dicranograptus, as generally supposed, but from Didymograptus. From the latter it is only separated by the presence of the solid virgula and the peculiar shape of the thecae. Both are probably secondary acquisitions, and the form, described here as Didymograptus incertus, appears to me to indicate the path of this derivation; for, though it is in all its appearance and by the presence of the dorsal thickening a Dicellograptus, it has the thecae of a Didymograptus. As the peculiar thecal shapes of the Upper Champlainic and Upper Siluric species are distinctly later acquisitions, appearing only toward the end of the graptolite reign, they are here of no phylogenetic significance.

If then the virgula of Diplograptus is an organ originating within the sicula and nemacaulus, and that of Dicellograptus an organ which originates within the walls of the coenosarcal canal of the branches, they can not be

homologous organs, though the mode of the formation of the virgula within the walls of the sicula of Diplograptus suggests that this virgula also was originally but a thickening of the periderm — of the nemacaulus however — and only afterward became more or less separated as a rod.

Since it is obvious that our stock of observed facts is not yet sufficient to solve either the problem of the relationship of the two largest divisions of graptolites, the orders Axonolipa and Axonophora, or that of the phylogenetic connection between the two large groups of graptolites which Frech has united under the caption Axonolipa, viz the Dendrograptidae and Dichograptidae, it appears that the present status of our knowledge of the differences between the Dendrograptidae, Dichograptidae and Axonophora would be best expressed by still recognizing all of them as independent orders.

*c* **Phylogeny of the genera and species.** Speculation as to the possible *phylogenetic relations of the genera of the Dendroidea*, Dictyonema, Desmograptus, Dendrograptus, Callograptus and Ptilograptus would be altogether premature, since these groups are based thus far largely on external characters which, in view of the complicated internal structure observed in several species, are probably inadequate to a correct understanding of their natural relations.

The problem of the *phylogeny of the Dichograptidae* has been the subject of investigation by Nicholson and Marr, whose work has been ably continued by Elles.

Nicholson and Marr [1895, p.529] observed that in the more ancient types of graptolites the thecae are comparatively simple, while in the later types, as Dicellograptus, Dicranograptus and Monograptus, they are much more complex. A number of groups can be discerned by the character of the thecae. From these facts they concluded "that the character of the thecae is the most important point to retain in separating families of the Graptoloidea," and that the next most important point to consider as indicating genetic relationship is the "angle of divergence," while, on the other hand, the number of branches in the rhabdosome, by which our present genera

of the Dichograptidae, as Tetragraptus, Didymograptus, Loganograptus, Dichograptus, are largely defined, is a character of minor importance.

They find that, when the Dichograptidae are separated into groups characterized by their thecae, (1) the different groups exhibit a series of parallel modifications as regards the number of branches in the rhabdosome, and (2) the older forms of the group are more complex, and the later forms undergo reduction in the number of branches.

To illustrate this important principle, the authors show that, of the nine species of Tetragraptus well known to them, "eight are represented by forms of Didymograptus which are closely comparable as regards the characters of the hydrothecae." It is further stated, that four of these four branched Tetragrapti are represented, as regards the character of the thecae and the amount of the angle of divergence, by forms of Dichograptus or Bryograptus.

The extraordinary resemblances between the various species of Bryograptus, Dichograptus, Tetragraptus and Didymograptus have led the authors to the conclusion that the species of these genera have not descended from a common ancestral form for each genus, but are the result of the variation of a number of different ancestral types along similar lines. These heterogenetic, homoeomorphous derivations, as they are termed by the authors, appear more or less simultaneously, a fact which has made them extremely valuable to the geologist. The explanation for the remarkable parallelism displayed in the reduction of multiramous, irregularly branching forms through multiramous regularly branching to pauciramous symmetric forms, among the Dichograptidae, is sought in the suggestion that symmetry in the arrangement of the branches would tend to insure an equal supply of food to each branch, and that the fewer the branches the greater the supply of food to the entire organism.

The suggestions of Nicholson and Marr on the phylogeny of the Dichograptidae have been made the subject of a most detailed investigation by Elles [1898, p.529ff]. This authoress, who states that in her study of the Skiddaw slate graptolites she has also been greatly impressed by the remarkable resemblances between species of different genera, has obtained

*Didymo*

*Tetragr*

*Multira*

SUGGESTED PHYLOGENY OF THE AMERICAN GRAPTOLOIDEA AXONOLIPA

and compared the thecal characters, and the measurements of the number of thecae within a certain space, of their inclination, apertural angle and overlap, and by means of these exact data confirmed the close resemblance of the characters of the thecae in members of different genera.

Miss Elles's investigations have led her to agree with Nicholson and Marr (1) that these resemblances are of *genetic origin*, and therefore (2) of *systematic value;* and further (3) that in any natural group the forms with relatively fewer branches were developed from the more complex forms; so that it follows from this (4) that the so called "genera" of the usually accepted classification of the Dichograptidae are far more of a *chronologic* than of a *zoologic* significance. Her own work has suggested the further conclusion that the forms in question are most probably the result of development along *certain special lines.*

Altogether eight groups with like thecal characters are recognized by Miss Elles among the Dichograptidae of the Skiddaw fauna. Some of these groups (five) are derived from the early multiramous genus Bryograptus, and the remaining three from Clonograptus. In each case the reduction in the powers of dichotomy leads first to a Tetragraptus and finally to a Didymograptus. As many of the forms are also represented in our Deep kill fauna, we cite these groups and invite the reader to test the similarity of the forms belonging to the same groups, as far as possible by using the plates.

(1) GRAPTOLITES DERIVED FROM BRYOGRAPTUS

(*a*) Bryograptus ramosus *var.* cumbrensis
*Tetragraptus pendens*
* Didymograptus indentus

(*b*) Bryograptus ramosus *var.* cumbrensis
*Tetragraptus fruticosus*
Didymograptus furcillatus

(*c*) Bryograptus ramosus *var.* cumbrensis
Tetragraptus postlethwaitii
*Didymograptus bifidus*

(*d*) *Tetragraptus bigsbyi*
T. phyllograptoides
*Phyllograptus angustifolius?*
*Didymograptus gibberulus*

(*e*) Bryograptus callavei
Tetragraptus *sp.* (Hincksii type)
*Didymograptus nicholsoni*
Azygograptus lapworthi
Didymograptus affinis
Azygograptus suecicus
*Didymograptus gracilis*

(2) GRAPTOLITES DERIVED FROM CLONOGRAPTUS

(*f*) * Dichograptus octonarius
*Tetragraptus serra*
* Didymograptus arcuatus
(*g*) *Loganograptus logani*
*Dichograptus octobrachiatus*
*Tetragraptus quadribrachiatus*
*Didymograptus extensus*
(*h*) * Tetragraptus headi
*Didymograptus patulus*

These groups can readily be arranged into genealogic trees or diagrams, as has been done by Miss Elles, the first of these having Dictyonema and the others Clonograptus as their basal form.

The forms which are constituents of the New York fauna are printed here in italics and those not reported from here, but found in Canada, are marked by an asterisk. This arrangement readily shows that the ancestral species of Bryograptus are foreign to this continent; but, on the other hand, some forms have been cited in the lists which have not yet been found in the Skiddaw slates. This would be expected in a class which, like that of the graptolites, has not developed in a small restricted area, but is of world-wide distribution, and the complete phylogeny of which could hence be obtained only by a comprehensive study of all the contemporaneous forms.

A closer inspection of the lists cited above demonstrates that there still exist considerable gaps and differences between some of the forms, which, for instance, between Bryograptus ramosus var. cumbrensis and Tetragraptus fruticosus, are so great — not only in general appearance but also in the character of the thecae — that a derivation of the latter from the former without existing intermediate forms is still hypothetic.

On the whole, however, the study of the succession and morphology of the Dichograptidae of the Deep kill fauna not only has corroborated the view of the British authors on the probable phylogeny of these forms, but has also furnished a considerable number of additional similarities between different species and genera, which are enumerated here:

(1) The series leading to Tetragraptus fruticosus is continued in the next horizon by T. clarkei.

The relation of these two species is discussed under the latter [p.653], and it is stated there that T. clarkei is a later, interesting derivative from

T. fruticosus, in which, by the process of acceleration in development, the flexure and widening of the branches have been transferred to their proximal portions.

(2) Didymograptus similis agrees in the characters of its thecae so closely with Did. extensus that it can safely be held to be a descendant of that species which has fallen below the size which the series attained at the time of its acmic development in the Tetragraptus horizon. Did. similis is found in the next two horizons, that with Did. bifidus and that with Diplograptus dentatus. It possesses inconspicuous sicula, the broad and short thecae of Did. extensus, the thecae number in both 9-10 within the space of 10mm, and the angle of inclination and overlap of the thecae do not differ materially; the overlap of the thecae is a little greater (two thirds to three fourths against one half to two thirds in Did. extensus), indicating a slight condensation of the thecae, while at the same time the total length of the branches has become greatly lessened.

(3) Didymograptus nitidus holds a position between D. patulus and D. extensus, both of which it approaches in some of its many slight varieties. With D. extensus it has in common the size of the sicula, inclination and overlap of the thecae, but differs in the considerably closer arrangement of the thecae. There is no Tetragraptus known in the Lower Siluric to which D. nitidus could be readily referred; and we incline to the opinion that it is a derivative from another species of Didymograptus, possibly D. extensus.

(4) Bryograptus lapworthi, Didymograptus nicholsoni and D. ellesi.

| | Characters of thecae etc. | Number of thecae in 10 mm | Inclination of thecae | Overlap |
|---|---|---|---|---|
| Bryograptus lapworthi | Slender forms; thecae with straight or slightly concave outer walls; apertures appear nearly straight | 10 | 15–20° | $\frac{1}{3}$–$\frac{1}{2}$ |
| Didymograptus nicholsoni | | 10–11 | 20° | $\frac{1}{4}$–$\frac{1}{3}$ |
| Did. ellesi | | 10–12 | 8–10° | $\frac{1}{4}$ |

The similarity between the first two species which is indicated by the measurements of the thecae, is still increased by the narrow, rigid and straight character of the branches, and their approximately equal angles of divergence as well in the proximal as also in the distal portions (110°-140° in Bryograptus lapworthi and 110°-130° in Didymograptus nicholsoni). The similarity between the rhabdosomes in our material is so close that, where only broken branches or young colonies are observed, the distinction between the two is very difficult.

Didymograptus gracilis is considered by Miss Elles to belong to the same series as D. nicholsoni. There exists indeed an unmistakable similarity in the habit of the form which is referred in the monograph of the British graptolites to D. gracilis Törnquist, to the species of Bryograptus and Didymograptus referred here to the same series. This similar habit is produced by the relative rigidity and straightness of the branches and their similar angles of divergence as well as the slender character of the thecae. We show however in the systematic part of this memoir [p.561] that the British form belongs to a different species, which it is here proposed to term D. ellesi. The last represents indeed a derivative of D. nicholsoni with looser arrangement of the thecae; while the typical D. gracilis, which is also present in our fauna, belongs to a different evolutionary series [p.561].

(5) D. spinosus is the only species of Didymograptus known to have possessed dorsal and apertural spines. There is however, also a species of Tetragraptus, T. acanthonotus Gurley, found in the Levis shales, which differs from the other species of Tetragraptus by the same features. Yet a comparison of the characters of the thecae brings out the fact that the latter species is a much coarser form, with uniformly wider branches, less closely arranged thecae (which is only coincident with the coarser structure of the whole colony) and more inclined thecae. It is hence doubtful whether the presence of the spines in both species indicates the parallel acquisition of a new character in the related forms or a closer phylogenetic bond.

(6) The peculiar Deep kill form, Goniograptus perflexilis, which is characterized by very long thecae, thin branches, very long branches of the first order ("funicle") and large divergence of the branches of the second order, bears an extremely striking similarity in general appearance to a somewhat more robust Dichograptus from the Skiddaw slates, viz Dichograptus separatus Elles.

The following table gives a comparison of the characters pertaining to their general appearance.

| | Length of branches of first order | Divergence of branches of second order | Divergence of branches of third order | Number of thecae in 10 mm | Width of branches |
|---|---|---|---|---|---|
| Goniograptus perflexilis | 6 mm | 90°–100° | 70°–80° | 6–7 | .4 |
| Dichograptus separatus | 6.35 mm | 105° | 70° | 13 | .5 |

If we, however, compare the characters of the thecae, we find that in Dichograptus separatus they are more closely arranged, and more inclined. As these differences are indicative of a condensation of the growth of the branches, they may not be so prohibitive of a phyletic connection between the two species as they would appear at first glance.

Indeed, a perusal of the tables of measurements of the thecae of the various supposed phyletic series distinctly brings out the fact, that in a large percentage of the groups the thecal arrangement shows progressive condensation in successive forms. To cite the more notable instances, the inclination of the thecae increases in the group leading from Bryograptus ramosus var. cumbrensis to Didymograptus indentus from 20° to 30°, in that leading from the same species to D. furcillatus from 20° to 45° and in that leading again from the same species to D. bifidus from 20° to 45°, while the number of thecae at the same time increases from 9-10 to 13-14 within 10 mm.

As the subequal length of the "funicles" of both species, Goniograptus perflexilis and Dichograptus separatus, is proof of

the originally equal dimensions of their thecae, the differences found in the closeness of arrangement and inclination of the thecae can, also, here be attributed with propriety to a condensation of the branches.[1]

(7) A small series of Tetragrapti and Didymograpti of the Deep kill fauna is characterized by projecting acute or mucronate apertures of the thecae. The accompanying table gives the detailed characters of the thecae of these.

| | Character of thecae | Number of thecae in 10 mm | Angle of divergence | Overlap |
|---|---|---|---|---|
| Bryograptus lapworthi | Thecae slender straight, with abruptly widening projecting apertures | 10 | 15°–20° | $\frac{1}{3}$–$\frac{1}{2}$ |
| Tetragraptus taraxacum | | 12 | 4° proximally; 40°–60° distally | $\frac{1}{4}$ proximally; $\frac{1}{2}$ distally |
| Didymograptus acutidens | | 11 | 15° | $\frac{1}{3}$–$\frac{1}{2}$ |
| Didymograptus cuspidatus | | 11–12 | 18° proximally; 40° distally | $\frac{1}{3}$–$\frac{1}{2}$ |

The table shows readily that the thecae of these species agree well in their arrangement, inclination and overlap. The last three named species are still more closely united by the character of the aperture, mentioned above, which attains its extreme development in Didymograptus cuspidatus, which also is the last appearing form of the series. Bryograptus lapworthi does not possess the typical apertural projections of the group. The fact, however, that in Tetragraptus taraxacum the first thecae also fail to present this character, but agree fully with those of B. lapworthi, is good

[1] The interesting problem of the tendency to a condensation of the thecae is treated more fully in another chapter [p.569].

evidence of the derivation of T. taraxacum from a form with the thecal characters of B. lapworthi.[1]

Bryograptus lapworthi can be considered as having descended through unknown intermediate forms from Staurograptus dichotomus var. apertus with some degree of certainty, springing from the fact that the character and arrangement of the thecae in the two species fairly agree (number of thecae 11–13 in 10 mm in S. dichotomus var. apertus; angle of inclination 25°; overlap $\frac{1}{3}$).

(8) A series with strong diagnostic characters is that leading from Goniograptus perflexilis through a peculiar flexuous, four branched form, Tetragraptus lentus, to Didymograptus filiformis and D. gracilis.

| | Character of thecae etc. | Number of thecae in 10 mm | Angle of inclination | Overlap | Width of branches |
|---|---|---|---|---|---|
| Goniograptus perflexilis | Thecae extremely long, narrow, very little widening, curved. Branches of first order originating near middle of sicula | 6–7 | 5° | $\frac{1}{2}$ | .4 |
| Tetragraptus lentus | | 6–10 | 5° | $\frac{1}{4}$ | .37 |
| Didymograptus filiformis Tullb. | | 8–10 | 10°–15° | $\frac{1}{4}$ | .25 |

The specific names of all four species express the thin, flexuous character of the branches, which is due to the extreme length (3 mm) and narrowness of the thecae, as well as to their small overlap (one fourth) and loose arrangement (6–10 in the space of 10 mm).

A peculiar character which these forms have in common with the Coenograptus series, also to be derived from Goniograptus perflexilis, is the origin of the branches about midway of the sicula.

[1] The change in the character of the thecae of T. taraxacum has been discussed by the writer in another connection [1902, p.589].

In Didymograptus filiformis and gracilis this feature is somewhat modified in so far as the two branches originate in unequal distances from the apex of the sicula, one in the middle and another a little more distally.

Didymograptus gracilis presents thin branches, long, narrow, little overlapping, remote thecae, similar to the members of this group; and, also, its first two thecae originate at different levels as in D. filiformis. It is, nevertheless, doubtful whether it represents more than a later parallelism to the forms of this series.

A comparison of the number of dichograptid species cited in the foregoing discussion and the considerably greater number of forms known from the Lower Champlainic graptolite beds, proves readily that still a considerable number of species, specially of the genera Tetragraptus and Didymograptus, have not been connected with older forms with a greater number of branches. Such a comparison will also show that the number of species increases considerably as we proceed from the earlier multiramous Clonograptus and Bryograptus toward Didymograptus. This stands, of course, in accordance with the general fact of the multiplication of types during the time of the progressive development of a race. As, hence, the number of known species of Didymograptus is considerably greater than that of Tetragraptus, it is evident that not every Didymograptus can have its Tetragraptus, and that either several species of Didymograptus have developed from the same species of Tetragraptus or species of Didymograptus have become themselves, the radicles for new species of the same genus. The latter alternative is strongly suggested by the great similarity of several species of Didymograptus among themselves, as among D. affinis and D. nicholsoni; or between D. extensus and D. nitidus; or between D. (gibberulus) caduceus and D. forcipiformis.

Our observation of the similarity between Clonograptus (Staurograptus) dichotomus and certain species of Bryograptus and of the fact that a laterally compressed Clonograptus can only with

difficulty be distinguished from a Bryograptus [p.616 and pl.2] suggest to us the inference that Bryograptus is derived from Clonograptus by a suppression of half of the primary dichotomies and a retention of the irregular branching. Moreover, the difference between the multiramous Dictyonema and the proximally biramous Bryograptus is still too great to warrant the assumption of a direct derivation without the intercalation of forms such as Clonograptus with fewer branches than Dictyonema has and more than Bryograptus has.

The great similarity in the exterior aspects of the proximal portions of the rhabdosomes of Clonograptus (Staurograptus) dichotomus and Dictyonema flabelliforme is pointed out under the description of these forms [*see also* pl.1, fig.15; pl.2, fig.9]. This is due to the similar initial branching and may be entirely accidental, but is certainly quite suggestive of a common ancestor in view of the presence of these two forms alone in the lowest graptolite bed.

For these reasons, we incline to the view that all Dichograptidae will be finally traced back to Clonograptus forms, from which one part develops through Bryograptus, the other through Loganograptus and Dichograptus, into Tetragraptus and Didymograptus stages.

The *Phyllograptidae* have, by Holm's investigation, been shown to be Tetragrapti of the recumbent series, the branches of which have coalesced with their dorsal sides. A transitional form, in which the proximal parts of the four branches also are said to be united, is reported under the name Tetragraptus phyllograptoides (Linnarsson ms) from Sweden [*see* Elles, p.534]. This would seem to lead from Tetragraptus bigsbyi to Phyllograptus angustifolius. Whether the other species of Phyllograptus branched off from this radical form of the group, or whether also the Phyllograptidae are of polyphyletic origin, has not yet been investigated. At any rate, no forms of Tetragraptus are known to which the other species of Phyllograptus, P. ilicifolius, P. typus and P. anna, could be readily referred. There seems to have taken place, not only a condensation of the branches and a resulting curving

and subradial arrangement of the thecae, but also a differentiation of the character of the apertures, which manifests itself principally in the varying development of the apertural mucros or spines.

In the absence of other species of Tetragraptus, which could be considered radicles of species of Phyllograptus, and the distinct succession of the forms in time, it is more probable that the Phyllograptidae form a compact, monophyletic group. Yet even in this small group it is evident that Phyllograptus ilicifolius and its successor, P. anna, are more closely related with each other than with P. angustifolius and P. typus.

A peculiar branch of the Dichograptidae, on whose genetic relations hitherto no light has been thrown, are the *Coenograptidae.* These do not appear till the Upper Champlainic, or Ordovicic horizons are reached. The path of their derivation has been pointed out by the discovery of an ancestral type of the family, viz Sigmagraptus praecursor [pl.5, fig.13] in the Deep kill fauna. This interesting form possesses two principal stems, from which undivided branches originate alternately on either side. The principal stems foreshadow already in their curvature the peculiar sigmoidal curve of those of Coenograptus. In Coenograptus the branches of one half of a rhabdosome are turned to one side, those of the other, turned to the opposite side. On well preserved specimens of C. gracilis [*see* text figure], I have however been able to observe that every second branch bends across the principal stem to the same side as the preceding branch, which makes the original arrangement of the branches identical with that of Sigmagraptus. Both have also in common the long, little overlapping, slender thecae and thin branches.

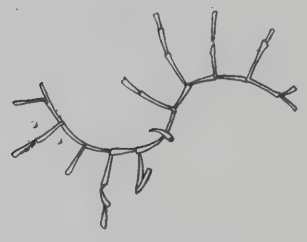

Fig. 15 Coenograptus gracilis Hall *sp.* x4 (Copy from Ruedemann)

A peculiar feature of Coenograptus as well as of Sigmagraptus is the divergence of the principal stems near the middle of the sicula, which leaves the apertural end of the sicula protruding fully beyond the stems.

The feature of a long aperturally projecting sicula we meet again as a marked characteristic of the two peculiar new forms here referred to Goniograptus as G. perflexilis and G. geometricus [pl.8, fig.15 and 39].[1] The former of these agrees in the length of the "funicle," length and low inclination of thecae, slenderness of branches and relative distance of their points of divergence from the principal stem, and their angles of divergence so closely with Sigmagraptus praecursor, that there is no doubt in my mind of the phylogenetic relationship of the two. [*See* following table of measurements]

| | Character of thecae and branches | Length of branches of first order | Number of thecae in 10 mm | Inclination of thecae | Overlap | Angle of divergence of branches | Width of branches |
|---|---|---|---|---|---|---|---|
| Goniograptus perflexilis | Thecae long, slender Slender branches | 4–6 | 6–7 | 5° | $\frac{1}{3}-\frac{1}{2}$ | 80° | .4 |
| Sigmagraptus praecursor | | 2.8 | 8–10 | 12° | $\frac{1}{3}$ | 90° | .3 |
| Coenograptus gracilis | | 2 | 8–10 | 5°–15° | $\frac{1}{3}-\frac{1}{2}$ | 90° | .5 |

Sigmagraptus praecursor originated from Goniograptus perflexilis by the failure of the first thecae to produce two principal stems each by dichotomy. The one branch developed has retained on either side of the sicula the oblique position to the "funicle," the result being the slightly sigmoidal curve of the principal stems.

[1] The same protrusion of the sicula beyond the point of origin of the branches and its resulting conspicuity, are found also though not so typically developed in another series of forms, to which Tetragraptus lentus, Didymograptus filiformis and D. gracilis belong [p.561]. Also, these forms are derived from Goniograptus perflexilis. It is further very notable in a small paracmic Tetragraptus [T. pygmaeus; pl.12].

While this conspicuity of the sicula is partly due to the slenderness of the thecae, its principal cause is the origin of the branches in all the forms at a point very near the apical end of the sicula [pl.12, fig.11] and the abrupt diverging of the mother thecae of the branches.

In the same way as Coenograptus is readily traced through Sigmagraptus to Goniograptus, which clearly is a derivative of Clonograptus, the genera Pterograptus and Pleurograptus, at present united with Coenograptus in a small separate group of Dichograptidae, also appear to be traceable to Clonograptus.

The last remaining genus of the Dichograptidae, represented in the New York fauna, is Temnograptus, a coarse multiramous form which at present can not be connected with any other genus, but, by exclusion, can be said to have been derived from some species of Clonograptus by transitional stages not yet known.

If we represent the supposed phylogeny of the Dichograptidae in the customary form of a tree and its branches [p.553] we find at the base the genus Clonograptus, from which one stem leads up through Staurograptus dichotomus var. apertus to Bryograptus, another through other forms of Clonograptus. From both of these arise numerous upshooting branches much as in stunted willow trees, some of which at times again send off twigs. If we lay a horizontal plane low down through these bundles of branches, it passes through forms which, though belonging to various offshoots or lines of descent, all have in one bundle the character of a Bryograptus and in the other that of a Dichograptus or a Goniograptus. Laying a higher horizontal plane through the branches, we intersect the forms all in the Tetragraptus stage, and the ultimate twigs are nearly all in the Didymograptus stage.

These horizontal planes represent a certain stage of development as for instance the Tetragraptus stage, passed through by all the series represented here as upshoots of Dichograptidae at approximately the same time in geologic history. At the intersections of the plane with the branches we find hence the species which, while belonging to different races, have all reached the same stage in the gradual reduction of the number of branches. These species have been grouped into the genera as they are at present understood. We have here, therefore, a remarkably distinct case of the law of parallelism in development.

Some peculiar side branches are, that leading through Goniograptus and Sigmagraptus to Coenograptus, another producing through Tetragraptus (bigsbyi) similis and others the Phyllograptidae, and the branch represented by the Temnograptidae.

The appended diagram is intended to illustrate these supposed phylogenetic relations of the species of the Dichograptidae and the character of the present genera as stages in a parallel development of various series. It is based on Nicholson's and Marr's, and Elles's suggestions, the phylogenetic diagram furnished by the last named author, and the observations of phyletic series in the New York fauna, cited above. We have, for reasons stated before, referred all forms to Clonograptus as a radicle, added the series recognizable in our fauna and restricted ourselves as much as possible to forms found either here or in the Canadian extension of the beds.

*d* **Supposed causes of the evolution of the Dichograptidae.** A study of the stages through which the various series of Dichograptidae pass during their parallel development shows that the whole race begins with multiramous, very irregularly branching forms and ends with pauciramous, very regularly branching and symmetric forms. This tendency makes itself manifest whether we follow a series leading from the Cambric Clonograptus through Goniograptus to Sigmagraptus and Coenograptus, or from the same genus to Temnograptus, or through Bryograptus to Tetragraptus and Didymograptus, or, finally, through Dichograptus to the same last named stages of development.

As explanation for this tendency, Nicholson and Marr suggest its connection with the supply of food. They argue that symmetry in the arrangement of the branches would tend to insure an equal supply of food to each branch; and that the fewer the branches, the greater the supply of food to the entire organism.

It strikes us that this suggestion does not take sufficient notice of the irregular branching, multiramous habit, insisted on by the Dendroidea, which, as Dendrograptus, were attached by thick stems, while such Dendroidea as Dictyonema flabelliforme, which were clearly suspended, become symmetric in their growth.

As, now, according to Lapworth's theory, the Dichograptidae were suspended forms, derived from sessile benthonic forms, it seems necessary for us to take into account the influence of the suspension from a mostly very thin thread — often indeed, as in Tetragraptus bigsbyi, etc., strikingly thin in relation to the size of the colony — on the gradual production of the symmetric arrangement of the branches. An irregular growth in a suspended colony is clearly liable to lead to a disturbance of the equilibrium of the colony, the consequent sinking of one half and rising of the opposite half of the rhabdosome and a resulting disarrangement of the normal position of the thecae. The nicety of balancing is hence quite plausibly one of the ends sought in the often rigidly symmetric arrangement of the branches.

The reduction of the number of branches, however, goes hand in hand with a lengthening of the remaining branches, so that the total length of the branches or of the number of thecae in the later pauciramous forms is not only not smaller but materially greater than in the early multiramous forms; for we see everywhere the numerous short branches of the Clonograptus and Bryograptus forms followed by the immensely long branches of the species of Loganograptus, Dichograptus, Temnograptus, Coenograptus and Tetragraptus. We can not for this reason believe that the reduction of the number of branches could have been for the purpose of increasing the food supply of the entire organism, but incline rather to the belief that this reduction was incidental to the assumption of the symmetric form.

If we contrast Clonograptus with its great power of branching by dichotomy with the last sprouts of the race, the species of Azygograptus, which are altogether unable to produce dichotomies, it appears that the tendency to a reduction of the number of branches finally became so fixed that the series shot, so to say, beyond the mark, and the power of branching was finally lost altogether.

A peculiar feature of the species of Didymograptus is, that those which are rigidly horizontal attain, at least in the Lower Champlainic fauna, a size

much surpassing that of the dependent, declined or reclined forms. This is exemplified specially by Didymograptus extensus, nitidus and patulus. As my material shows that these forms also possessed but an extremely short, if any, nema, and that the primary disk, which was large, was closely affixed to the sicula and to the center of the colony, the inference is very plausible that these long branches were closely adhering to the underside of floating objects, perhaps seaweeds, similarly as the colonies of some bryozoans are at present. In the Upper Champlainic appear also dependent, or rather flexuous types of Didymograptus with branches of astonishingly large linear dimensions.

Another tendency of development, becoming manifest among the Dichograptidae and incidentally mentioned above, is that of condensing the branching by a close arrangement of the thecae. This is largely accomplished by giving the thecae a more oblique position to the axis of the branch. The gradual increase in the angle of inclination in several series has been pointed out above [p.559].

The branches of several species recapitulate this process in their individual ontogenetic development, as we have shown in a former paper [1902, p.587] in the cases of Goniograptus thureaui and Tetragraptus fruticosus. In these forms the branches begin with long slender thecae, with a small angle of inclination. As a rule gradually, but sometimes quite abruptly, as in T. fruticosus, the thecae become more closely arranged by a decrease of overlap, and more inclined. In the later species they also become provided with apertural mucros, which must be a later acquisition of the series [*see* fig.11, p.531].

The cause of the condensation of the branches is to be found in the reclined position assumed by them in an endeavor of the rhabdosomes, which have become suspended, to restore to the zooids their original erect position. By this ascending growth of the branches, they lengthen in the direction of the point of fixation or support, whatever this may have been, thus necessitating a corresponding lengthening of the supporting nema and thereby endangering, by undue longitudinal growth, the fixation

of the colony. It was hence of advantage to shorten the branches in the forms where they are reclined. For this reason we find the broad, short branches in Tetragraptus (bigsbyi) similis and Didymograptus (gibberulus) caduceus, species in which, and in the Phyllograptidae, the reclining has gone the farthest.

*e* **Classification adopted here.** We have shown in the preceding discussion that the phylogenetic relations of the principal groups are not yet elucidated, while those of the families and genera as far as known indicate the necessity of a future revision of the present more or less artificial groupings. It would, under these circumstances, be premature to attempt new classifications; and we use here that still in general use and based on Lapworth's *Improved Classification of the Rhabdophora*, with such modifications as are suggested by later investigations, and which we cite here briefly.

Lapworth comprised under the Rhabdophora all graptolites with the exception of the dendroid forms, at that time still doubtfully referred to the graptolites. For the latter the term Dendroidea proposed by Nicholson is currently used. The Rhabdophora were divided by Lapworth into the Graptolitidae and the Retioloidea.

As is indicated by the similarity of the thecae of various Retioloidea to those of forms of Diplograptus and Climacograptus, and by the early appearance, in Retiograptus, but late acmic development of the group as a whole (after that of the Diplograptidae proper), this group is of polyphyletic origin and composed of terminals of various series which have adapted themselves in a parallel manner to the floating habit of the graptolites [p.518]. We have, for this reason, not recognized here the order Retioloidea but united the single representative in our fauna (Retiograptus) with the Climacograptidae.

Frech has divided the graptolites into two orders, the Axonolipa and Axonophora, according to the absence or presence of an axis. While we have noted before [p.552] that this axis may not in all genera be a homologous organ, and hence its recognition as a diagnostic character is

not irreproachable, there is little doubt that by it two groups of the Graptoloidea can be distinguished, which also differ in other structural features and which are separated in time. These are the Dichograptidae and Diplograptidae in their widest sense. Frech, however, unites under the Axonolipa the Dendroidea and the Dichograptidae, two groups which, by the character of their thecae and their mode of growth, appear to us too widely separated to be united with propriety in one order. We have for this reason, retained the original division into the orders Dendroidea and Graptoloidea, and divided the latter into the suborders Graptoloidea Axonolipa and Graptoloidea Axonophora. Neither of these principal groups can, at present, be genetically connected with any of the others, while the closer genetic relation of their subdivisions is little to be doubted.

(1) The order Dendroidea is represented in our fauna by the family Dendrograptidae with the genera Dendrograptus, Dictyonema, Desmograptus, Callograptus and Ptilograptus.

(2) The order Graptoloidea is divided into the suborders $B_1$ Graptoloidea Axonolipa and $B_2$ Graptoloidea Axonophora.

The suborder Graptoloidea Axonolipa comprises the provisional family, Dichograptidae *sensu stricto*, the Phyllograptidae and Coenograptidae. The Dichograptidae will eventually be divided into the series of genetically connected forms discussed above. For the present it seems most practical to retain the old terms Clonograptus, Bryograptus, Goniograptus, Loganograptus, Dichograptus, Tetragraptus and Didymograptus.

The small family Phyllograptidae contains but one genus, Phyllograptus.

A family, Leptograptidae, was erected by Lapworth to receive the genera Coenograptus, Nemagraptus, Pleurograptus, Amphigraptus and Leptograptus. Our material has demonstrated that Coenograptus gracilis, the type of the genus, is derived by a new form of generic value for which we have proposed the term Sigmagraptus, from a Goniograptus.

A peculiar new tenuous tetragraptid form, here described as

Etagraptus lentus, indicates quite distinctly the separate path of the evolution of at least one of the thin biramous graptolites with very remote slender thecae. The family Leptograptidae appears hence to comprise several entirely different evolutional series. We have for this reason separated one of these as the Coenograptidae.

Also the genera grouping themselves around Temnograptus are very liable to be found eventually to constitute a separate family, which is characterized by peculiarities of branching. The New York fauna contains only a single representative of the genus Temnograptus.

The suborder Graptoloidea Axonophora does not appear till the time of the last of the zones, whose faunas have been here investigated, and it does not attain its principal development till the late Lower Siluric and the Upper Siluric.

Frech has separated the Climacograptidae from the Diplograptidae Lapw. and referred the genus Retiograptus to the Climacograptidae. As the direction of growth and shape of the thecae in Climacograptus are very different from those found in Diplograptus, this separation seems well supported by the facts and is adopted here.

With the Diplograptidae have here been united the genera Glossograptus and Trigonograptus, the latter with some doubt arising from the peculiar direction of the aperture, which is different from that of other Diplograptidae.

We thus obtain the systematic arrangement of the New York forms, which is given in the following synoptic list of our species.

*Synoptic list of fossils described*

Order 1 DENDROIDEA Nicholson

Family DENDROGRAPTIDAE Roemer

Genus DENDROGRAPTUS Hall

Dendrograptus flexuosus *Hall*
D. (?) succulentus *sp. nov.*
D. fluitans *sp. nov.*

Genus CALLOGRAPTUS Hall

Callograptus salteri *Hall*
C. *cf.* diffusus *Hall*

Genus PTILOGRAPTUS Hall

Ptilograptus plumosus *Hall*
P. geinitzianus *Hall*
P. tenuissimus *sp. nov.*

Genus DICTYONEMA Hall
Dictyonema flabelliforme *Eichw.* sp
D. murrayi *Hall*
D. furciferum *sp. nov.*
D. rectilineatum *sp. nov.*

Genus DESMOGRAPTUS Hopkinson
Desmograptus cancellatus *Hopkinson* sp.
D. intricatus *sp. nov.*

Order 2 GRAPTOLOIDEA Lapworth
Suborder A GRAPTOLOIDEA AXONOLIPA (Frech) Ruedemann *em.*

Family DICHOGRAPTIDAE *auct.* Frech *em.*

Genus STAUROGRAPTUS Emmons
Staurograptus dichotomus *Emmons*
S. dichotomus *var.* apertus *var. nov.*

Genus CLONOGRAPTUS Hall
Clonograptus *cf.* flexilis *Hall* sp.

Genus GONIOGRAPTUS McCoy
Goniograptus thureaui *McCoy*
G. geometricus *sp. nov.*
G. perflexilis *sp. nov.*

Genus LOGANOGRAPTUS Hall
Loganograptus logani *Hall*

Genus DICHOGRAPTUS Salter
Dichograptus octobrachiatus *Hall* sp.

Genus TEMNOGRAPTUS Nicholson
Temnograptus noveboracensis *sp. nov.*

Genus BRYOGRAPTUS Lapworth
Bryograptus lapworthi *sp. nov.*
B. pusillus *sp. nov.*

Genus TETRAGRAPTUS Salter
Tetragraptus quadribrachiatus *Hall* sp.
T. amii *Lapw.* (*Elles & Wood* em.)
T. fruticosus *Hall* sp.
T. clarkei *sp. nov.*
T. pendens *Elles*
T. serra *Brongniart* sp.
T. similis *Hall* sp.
T. woodi *sp. nov.*
T. taraxacum *sp. nov.*
T. pygmaeus *sp. nov.*
T. lentus *sp. nov.*

Genus DIDYMOGRAPTUS McCoy
Didymograptus extensus *Hall* sp.
D. nitidus *Hall* sp.
D. patulus *Hall* sp.
D. similis *Hall* sp.
D. gracilis *Törnquist*
D. acutidens (*Lapw.*) *Elles & Wood* em.
D. cuspidatus *sp. nov.*
D. nicholsoni *Lapw. var.* planus *Elles & Wood*
D. filiformis *Tullberg*
D. ellesi *sp. nov.*
D. törnquisti *sp. nov.*
D. spinosus *sp. nov.*
D. bifidus *Hall sp.*
D. nanus *Lapworth*
D. caduceus *Salter, Ruedemann* em.
D. forcipiformis *sp. nov.*
D. incertus *sp. nov.*

Family COENOGRAPTIDAE nom. nud.

Genus SIGMAGRAPTUS gen. nov.
Sigmagraptus praecursor *sp. nov.*

Family PHYLLOGRAPTIDAE Lapworth

Genus PHYLLOGRAPTUS Hall
Phyllograptus ilicifolius *Hall*
P. typus *Hall*
P. angustifolius *Hall*
P. anna *Hall*

Incertae sedis:

Genus STROPHOGRAPTUS gen. nov.
Strophograptus trichomanes *sp. nov.*

Suborder B GRAPTOLOIDEA AXONOPHORA Frech

Family DIPLOGRAPTIDAE Lapworth

Genus DIPLOGRAPTUS McCoy
Diplograptus dentatus *Brongniart* sp.
D. inutilis *Hall*
D. laxus *sp. nov.*
D. longicaudatus *sp. nov.*

Genus GLOSSOGRAPTUS Emmons
Glossograptus hystrix *sp. nov.*
G. echinatus *sp. nov.*

Genus TRIGONOGRAPTUS Nicholson
Trigonograptus ensiformis *Hall* sp.

Family CLIMACOGRAPTIDAE Frech

Genus CLIMACOGRAPTUS Hall
Climacograptus pungens *sp. nov.*
C. ? antennarius *Hall*

Genus RETIOGRAPTUS Hall
Retiograptus tentaculatus *Hall*

Appendix. GRAPTOLITHI *incertae sedis*

Genus CARYOCARIS Salter
Caryocaris *cf.* curvilineatus *Gurley*

Genus DAWSONIA Nicholson
Dawsonia monodon *Gurley*
D. tridens *Gurley*

## 11 Taxonomic relations of the graptolites

An exhaustive discussion of the probable taxonomic relations of the graptolites to other classes of organisms does not lie within the scope of a work on the faunas of a limited district. As the question concerning these relations is however a very pertinent one, and has not since Hall's memoir, been touched in the American literature, we notice here briefly the present status of the problem.

Hall insisted strongly, as Portlock did before him, on the sertularian affinities of the graptolites. Also the succeeding investigators who made a thorough study of the graptolites, notably Carruthers and Nicholson, maintained the hydroid relations in their publications. Allman, who treats the possible affinities of the graptolites most exhaustively in his *Monograph of the Gymnoblastic Hydroids*[1] came to the conclusion that "on the whole it would seem that the graptolites constitute a very aberrant hydrozoal group having manifest affinity with the Hydroidea, to which they are

[1] Also printed in Ann. and Mag. Nat. Hist. ser 4. 1872. 9: 364–80.

connected by the nematophore-bearing genera of the latter, while they have also important points of connexion with the Rhizopoda."

The facts which, in Allman's opinion and that of his contemporaries, most obviously opposed themselves to the acceptance of the hydroid affinities of the graptolites were the presence of a solid axis (the virgula) and the unconstricted mode in which the thecal cavity opens into the coenosarcal canal. In regard to the first fact, Rhabdopleura, a living bryozoan, which stands apart from the others by the possession of just such an axis, is pointed out to show that the graptolites, while provided with such axes, might nevertheless have preserved in all respects a typical hydroidal structure. We may emphasize here what, at the time when Allman's discussion was written, was not yet known, namely that only a suborder of the Graptoloidea, the Axonophora, possesses this axis, that the same is hence a late acquirement and not a diagnostic character of the class.

On account of the absence of the constriction at the basis of the thecae, Allman compares these, not with the hydrothecae which shelter the zooids, but with the calycles which contain the nematophores of the Plumularidae. The nematophores consist of nothing but protoplasm which has the power of emitting pseudopodia. The fact of the presence of dimorphic thecae in the Dendroidea, discovered since, would seem to lend support to the possibility of the suppression of one of these thecal forms in the Graptoloidea.

More recently however writers have been less positive in their views and have emphasized specially the following facts. (1) That the graptolites not only begin very early in the Upper Cambric but even become extinct in the Middle Devonic, that hence an enormous lapse of time separated the hemera of the graptolites and that of the sertularians and of other Hydrozoa, of which fossil remains are known only from relatively young formations. (2) It is, as Neumayr [*Stämme des Thierreichs*, p.346] has stated lucidly, a wrong tendency to endeavor to fit all fossil forms into the system of living organisms, a tendency which not only leads to forced and

unsafe, or even wrong correlations, but also gives a wrong conception of the development of the organic world, namely that of a great monotony, by which paleontology would not be enabled to make us acquainted with wholly new groups of forms.

Wiman also strongly urges that the graptolites can not be brought under any of the now existing classes of animals. To the placing of the graptolites with the Hydroidea, this author objects on the ground that first there is no hydroid known which has the structure of a graptolite, and secondly the persons of the first order of the graptolites (the thecae) are bilateral symmetric, while those of the Hydroidea possess a higher symmetry.

The possible objection that hydroid thecae also possess a bilateral symmetry is met by the statement that this can be explained by the position of the individuals, while in the graptolites the sicula already possessed a bilateral symmetry. But it is not to be overlooked here that one of the principal features which constitute the bilateral symmetry of the sicula, viz the position of the virgula within one of the walls, is clearly a later acquisition of the colony, for the earlier forms have no solid virgula, and it has hence by acceleration of development been transferred to the sicula. In a rapidly developing group such as the graptolites manifestly were, it is equally possible that the bilateral symmetry of the thecae, originally induced by their position, became so quickly fixed that by tachygenesis it appeared already in the sicula in a manner similar to the appearance of the virgula.

It is, further, to be considered that the sicula consists of two parts, an apical and an apertural one. The latter, which is the bilateral symmetric one, had clearly the properties and functions of a theca [p.520]; while the initial or apical part, which lacks growth lines, was the original embryo sheath. The latter, however, shows to my knowledge, a higher symmetry than a bilateral one; and such higher symmetry was hence, probably, also possessed by the embryo.

Like Neumayr and Wiman, Frech also holds that it can not be expected that the graptolites will show any close relationship to any living class of forms; but urges that one should rather expect to find the terms Hydrozoa and Anthozoa, based on living forms, unapplicable to the paleozoic types; and, on noting an analogy between the embryonal development of the Axonolipa and that of the tabulate corals, suggests that these together with the Stromatoporidae occupied the place of the present Hydrozoa. It is added, however, that whoever desires to force the graptolites into the present zoologic system, must place them near the Hydrozoa.

We fully agree with the last named author that it would be misleading to attempt to unite the graptolites with any class of living forms, but at the same time wish to emphasize the necessity of using a group of similar forms as means of reconstructing, if only by analogies, the picture of the organism and thereby gaining new working hypotheses to stimulate investigation. Thus Frech discusses most fully the relations and differences between the graptolites and the Plumularidae, and that directly after the statement that the graptolites can not be expected to be fitted into a class of living forms.

Moreover, even if an extinct group can not directly be placed within the confines of a class of living forms, it must naturally be more nearly related to one group of organisms than to all others that exist at present; and there is certainly much gained for the understanding and elucidation of the extinct forms, if this group is found. In this sense the present writer adduced the Siphonophora for comparison, when describing the pneumatocyst of Diplograptus; and later on emphasized the close similarity between the generative cysts observed in Diplograptus and the "gonangia" of the sertularians; and for the same reason the Hydrozoa have been used throughout this treatise as a standard by comparison with which an understanding of the graptolites is sought.

## DESCRIPTIONS OF GRAPTOLITES

### Order 1 DENDROIDEA Nicholson

### Family DENDROGRAPTIDAE Roemer

#### DENDROGRAPTUS Hall. 1865

The genus Dendrograptus was erected by Hall for forms with a strong main stem and a broad, spreading, shrublike, variously ramifying frond. The thecae are described as quite distinct and angular in some (the type species of the genus, D. hallianus Prout), of obscure form in others, while in still others they are shown only as round or elliptic pits or pustules.

Wiman [1895, 1900] has been able to isolate and investigate under the microscope four different forms which he refers to this genus. These possessed an internal structure similar to that in Dictyonema, viz a composition of three different kinds of thecal tubes, representing, according to Wiman, nourishing, and budding individuals and gonangia [p.592]. In those three of these four species which also from their external characters would be readily placed with Dendrograptus, all branches are simple, i. e. consist of but one series of individuals.

There is no doubt that eventually the internal structure will furnish the means of recognizing the phylogenetic relations of the forms united under Dendrograptus and of procuring thereby the criteria for a sharp and natural division or dissolution of the genus, which clearly contains very different elements. It has evidently been made the receptacle of all arboriform graptolites; and the fact of the great difference of the thecal apertures mentioned by Hall, in the original description of the genus, indicates already its heterogeneous character. We see at present no other way than referring a species like the D. ? succulentus of this paper to this genus, as there is no other designation extant for similarly constructed forms, and it would be unwise to undertake the dissolution of the genus by external characters, at a time when it becomes probable that the internal characters will furnish safer criteria for such a proceeding.

The habits of the forms of the genus indicate more than those of any others a sessile mode of life, for the stout trunk and the irregular ramifications remind so strongly of the structure of recent sessile hydrozoans that this similarity has frequently been cited as suggestive of a like mode of life of at least these forms. Moreover, there have been observed basal expansions of the stem, assuming the form of irregular bulbs or disks, which also would be most readily explained as organs of attachment. It is however to be remembered that no cases of actual attachment and fixation have yet been recorded, and that, at the Deep kill at least, and also in the Quebec shale and apparently in Wales, the species of Dendrograptus occur in the same facies and associated with all the other graptolites, as Dictyonema, Diplograptus, Climacograptus.

### **Dendrograptus flexuosus** Hall

Plate 4, figure 5, 6, 8-10

Dendrograptus flexuosus Hall. Canadian Organic Remains, decade 2. 1865. p.127f, pl.17, fig.1, 2

Dendrograptus flexuosus Hopkinson & Lapworth. Quar. Jour. Geol. Soc. 1875. 31:662f, pl.36, fig.3a-3d

Dendrograptus flexuosus Roemer & Frech. Lethaea palaeozoica, Bd1. 1897. p.578

Dendrograptus cf. gracilis Ruedemann. N. Y. State Paleontol. An. Rep't 1902. p.555

*Description.* Rhabdosome broadly flabellate (or infundibuliform?), attaining a length of an inch or more. Branches radiating from a short, stout nemacaulus, slender, flexuous, bifurcating frequently and somewhat regularly, diverging at first under a considerable angle, but soon becoming subparallel, the distal ones somewhat undulating. Thecae numbering 6–14 in 10mm; long, narrow, projecting distinctly, inclined at an angle of about 20°; apertural margin forming an angle of 80° with the axis of the branch.

*Position and localities.* Common in graptolite bed 2 (Tetragraptus zone) and rarer in graptolite bed 3 (zone with Didymograptus bifidus) at the Deep kill.

Hall's types came from a coarse, greenish shale at Point Levis, in which it is associated with Tetragraptus serra, Phyllograptus typus and Dendrograptus fruticosus. It may, hence, hold there the same position as at the Deep kill. Lapworth, Gurley and Ami did not observe it among the Canadian forms; data as to its exact horizon can not therefore be obtained from their lists. Hopkinson and Lapworth record it from their Lower Arenig of the Road Uchaf, Ramsey island and the Middle Arenig of Whitesand bay.

*Remarks.* From the mode of compression of certain specimens [fig.6], in which the branches are more crowded toward the marginal portions of the frond, and from the more or less circular disposition of the branches around the center in others, it would appear that the rhabdosome did not always lie fanlike in one plane, but may have grown infundibuliform.

This species is characterized by the numerous and close bifurcations and the greater divergence of the proximal parts of the divisions when compared with the more distal ones, a feature which becomes still more accentuated in D. divergens. Separated fragments of the rhabdosome offer quite varying aspects according to their original distance from the base. Very delicate fronds have been observed [fig. 7 and 8] in which the branching is very close and the thecae also very closely arranged (as many as 14 in 10mm), while in other features they do not differ from coarser fragments of the basal portions. As a quite perfect specimen, figured by Hopkinson and Lapworth [fig.3b, *ibid.*] shows the rhabdosome to divide distally into a mass of closely arranged delicate branches, these finer branched fronds have here been directly united with the coarser and broader branches in the same species.

A still more striking contrast between broad, short, basal branches and rather abruptly dividing tufts of finer branches, was observed in a new species from the horizon with Diplograptus dentatus, viz D. (?) succulentus.

The great difference in the remoteness of the thecae between different portions of the rhabdosome is shown in figure 9.

### Dendrograptus (?) succulentus sp. nov.

Plate 4, figures 1-4

Dendrograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* Rhabdosome very robust in its basal parts, branching very irregularly, often so frequently that the successive branches are nearly in contact; angles of branching very different in the basal parts; branches abruptly breaking up into pendent tufts of frequently dividing branchlets. Thecae not projecting; thecal apertures small, circular depressions, which in the basal parts are found apparently irregularly distributed around the entire circumference of the branches, while on the thin branches a serial arrangement is indicated. On the latter they number 8 to 10 in 10 mm. Where the external periderm of the branches has become exfoliated, their composition of fine tortuous thecal tubes is observable.

Fig. 16 Dendrograptus (?) succulentus sp. nov. Fragment which shows the composition of the branches of numerous tubes. Deep kill. x3.75

*Position and localities.* Common at the Deep kill in the shale of the horizon with Diplograptus dentatus.

*Remarks.* This species is easily distinguished from any other species of Dendrograptus known to the writer from the American Lower Siluric. D. serpens Hopkinson and Lapworth from the lower Llandeilo of Abereiddy bay in Wales [1875, p.665] is also characterized by robust basal branches and pendent terminal tufts of branchlets. From that younger species the Deep kill form is readily distinguished by its less diffuse habit, much closer branching and more rigid and ascending character of the branches; and the much more rapid decrease in thickness of the more distal branches. D. erectus Hall, from the Point Levis Tetragraptus shales, of which only the basal part is known, possesses also ascending branches; the latter are however neither so closely arranged nor so thick and robust as in D. succulentus.

The species received its name from the extremely broad branches, which, however, have become entirely flattened, giving them the impression of having been very thick but not very firm. It is quite apparent that these branches of massive appearance were only the basal parts of a multiramous form, which gradually tapered into the more delicate distal parts, and that the latter are retained only in exceptional cases, as in the tuft on the specimen represented in figure 4.

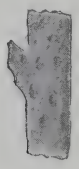

Fig. 17 Dendrograptus (?) succulentus sp. nov. Part of principal stem of specimen reproduced on plate 4, figure 4, enlarged to show arrangement of apertures. Deep kill. x5

It is doubtful whether this form can be properly referred to Dendrograptus with D. halli-anus Prout as the genotype, for the branches show no trace of "denticles" or thecae, but seem to be composed of bundles of fine tubes, opening without projections on the surface of a common periderm. Hall, however, has expressly drawn the limits of his genus so wide as to embrace forms in which the cellules "appear as simple indentations on the surface and those in which they are distinctly angular with the denticles conspicuous," and Hopkinson and Lapworth [1875] have referred like forms to Dendrograptus. It is however obvious that these forms differ essentially from species with projecting thecae, such as D. flexuosus.

### Dendrograptus fluitans sp. nov.

Plate 4, figures 11, 12

Dendrograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.555

*Description.* Rhabdosome small (?), consisting of thin, flexuous stems which bifurcate rather irregularly and terminate in long, filiform branches. Thecae narrow, three times as long as wide, closely arranged, numbering 16 in 10 mm; apparently only a short distance in contact with each other (about one fourth of their length); in the compressed state appearing as acutely pointed, little inclined (about 20°) denticles; outer margin concave, apertural margin slightly convex, recurving, forming an angle of 48° with the axis of the branch.

*Position and localities.* Rare in graptolite bed 2 of the Deep kill section, belonging to the Tetragraptus horizon.

*Remarks.* Only incomplete rhabdosomes have been observed. These suggest a form similar in its habit to Hall's D. flexuosus from the Levis beds of Quebec. The latter type bifurcates, however, more frequently and regularly, and has thecae arranged less closely by one fourth and differently shaped, with more obtuse apertural processes and angles. In the corresponding Skiddaw horizon no Dendrograptus has been found.

### CALLOGRAPTUS Hall. 1863

Since the erection and definition of the genus Callograptus by Hall in his work, the *Graptolites of the Quebec Group*, very little has been added to his observations on the genus. This is largely due to the fact that no more representatives of the same have been found, with the exception of two new species recorded by Hopkinson and Lapworth from Ramsey island [1875].

Hall based his genus mainly on its mode of branching and the resulting aspect of the rhabdosome; stating that it has "numerous slender bifurcating branches proceeding from a strong stem or axis," and that in its aspect it is intermediate between Dictyonema and some forms of Dendrograptus; that the branches are sometimes distantly and irregularly united by transverse dissepiments, but that the frond has not the regular, reticulate structure of Dictyonema and differs from Dendrograptus in the mode of branching and the form of the thecae.

The microscopic investigations of Wiman, which have resulted in the demonstration of the composite character of the thecal structures of both Dictyonema and Dendrograptus, have for lack of suitable material not been extended to this genus, and its actual relations to either Dictyonema or Dendrograptus are still unknown. Hall's material did not permit him to determine the character of the thecae, the latter appearing as simple oval impressions on the surface of the compressed branches.

While the shale material of the Deep kill is not suited for an elucidation of the internal structure of the branches, the observation of smaller pores

seems to indicate that their composition is similar to that found by Holm and Wiman in Dictyonema; or that there exist, besides the larger thecal tubes, smaller ones which have separate apertures as in Dictyonema, and that they do not empty into the thecae as in Dendrograptus. While Hall described the apertures as being located alternatingly on opposite margins, his somewhat diagrammatic drawing shows them in regular series. In the Deep kill material the apertures are irregularly scattered, or found disposed in a manner suggestive of a long spiral distribution.

### **Callograptus salteri** Hall

Plate 3, figures 13-15

Callograptus salteri Hall. Canadian Organic Remains, decade 2. 1865. p.135, pl.19, fig.5–8

Callograptus salteri Hopkinson & Lapworth. Quar. Jour. Geol. Soc. 1875. 31:667, pl.34, fig.10

Callograptus salteri Gurley. Jour. Geol. 1896. 4:300

Callograptus salteri Roemer & Frech. Lethaea palaeozoica, Bd 1. 1897. p.577

Callograptus salteri Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.554, 555, 565

*Description.* Rhabdosome infundibuliform, its outer margins forming an angle of 40°-50°. Branches springing from a thin, flexuous hydrorhiza without the intervention of a coarser stem; thin (.5 mm *ad max.*), numerous and closely arranged, the interspaces being less than the width of the branches; flexuous to undulating, bifurcating at irregular intervals, the resulting branches diverging but slightly and assuming immediately subparallel directions; rarely connected by dissepiments. Thecal apertures circular, little projecting, arranged in irregular series, numbering 14 to 18 within 10 mm; smaller pores observable between the larger apertures. Often longitudinally striated, where the thecal tubes have been pressed through the periderm.

*Position and localities.* Fragments of this species are, at the Deep kill, common on slabs of graptolite bed 2 (Tetragraptus horizon), but have also been observed on those of graptolite beds 1 and 5.

Hall states that his originals came from the Quebec group at Gros Maule in Canada. As we also find Dichograptus octobrachiatus, Tetragraptus serra, Didymograptus constrictus and Callograptus elegans recorded from that locality, the Tetragraptus horizon, or a subhorizon close to it, is probably exposed there; and this species occurs, hence, there at about the same level as here. Gurley has, indeed, observed both species, C. salteri and C. elegans, only in the "Main Point Levis zone," which is the Tetragraptus zone. Lapworth and Ami have not noticed this form among the collections of the Canadian Geological Survey. Hopkinson and Lapworth identified graptolites from the Middle Arenig of Whitesand bay, St Davids, Wales, with C. salteri and C. elegans.

Fig.18 Callograptus salteri Hall. A fragment with lateral views of thecae. Deep kill. x 5.25

Prof. H. F. Cleland has sent me a quite poorly preserved graptolite from the Beekmantown beds at Tribes Hill, in the Mohawk valley, which appears to be identical with this species.

*Remarks.* While fragments, found in the Deep kill shales, indicate that the branches attained the length and width observed by Hall in the material from Gros Maule, none of the specimens approach the robust character of the specimens figured under this specific designation by Hopkinson and Lapworth as coming from the Middle Arenig of Whitesand bay in Wales.

Fig.19 Callograptus salteri Hall. Enlargement of portion of rhabdosome to show the thecal apertures. Deep kill. x 5.25

Hall described this form as having a flabelliform rhabdosome, but stated under the generic description that it is possible that some of the species of this genus may have grown in funnel-shaped rhabdosomes as Dictyonema. The specimen of C. sal-

teri, figured here on plate 3, figure 15, appears to support this suggestion, at least in regard to this species.

The specimen just mentioned is further remarkable for its exhibiting a distinct, flexuous nema and a sicula. Older individuals of this species possess undoubtedly a robust main stem, from which the branches spring and which terminates proximally in a spreading fibrous hydrorhiza, as it has been found in the congeners of the species, notably C. elegans and C. radicans.[1]

### Callograptus cf. diffusus Hall

Plate 4, figure 7

Dendrograptus? (Callograptus?) diffusus Hall. Canadian Organic Remains, decade 2. 1865. p.132, pl.18, fig. 1-3

Dendrograptus? diffusus Hopkinson & Lapworth. Quar. Jour. Geol. Soc. 1875. 31:664, pl.36, fig.7a, 7b

Callograptus diffusus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* There occur in the shale with Phyllograptus typus, at the base of the horizon with Didymograptus bifidus, and in zone 3, branches of a dendroid graptolite which possess the characteristics of Dendrograptus? (Callograptus?) diffusus Hall, viz they are rather strong and rigid, frequently bifurcating and slightly bending at the bifurcations, the resulting branchlets strongly diverging. The thecal apertures, which number about 16 in 10 mm, are arranged in one, somewhat tortuous series, on the flattened branch and circular to oval in outline. The thecae are not projecting.

*Position and localities.* Rare in zones with Didymograptus bifidus and Diplograptus dentatus at the Deep kill.

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[1] By Hopkinson, Ann. & Mag. Nat. Hist. ser. 4, 10:233, pl.10. We have, therefore, probably here the same conditions which have been observed by the writer to have existed in Dictyonema flabelliforme [p.595], namely suspension by a thin filiform nema in the earlier growth stages and fixation by a shorter stout stem in the later stages.

*Remarks.* This species was described by Hall as being associated at Point Levis with Climacograptus antennarius, etc., i. e. with forms of the horizon of Diplograptus dentatus. Hopkinson and Lapworth identified with Hall's species a form obtained by them from the Lower Arenig of Road Uchaf, Ramsey island, Wales. As they also obtained Trigonograptus ensiformis at the same locality it apparently occurs in Wales at the same horizon as at Quebec and at the Deep kill, but may, as indicated by the occurrence at the latter place, appear already in the preceding horizon.

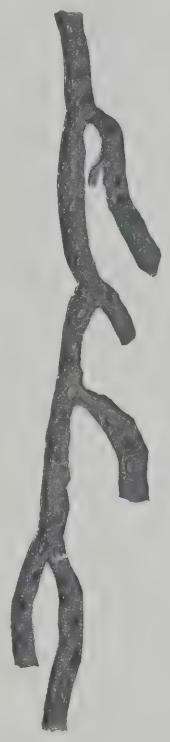

Fig.20 Callograptus cf. diffusus Hall. Enlargement of branch to show the thecal apertures. Deep kill. x 5.25

Hall did not reach any definite conclusion as to the generic position of the species; Hopkinson and Lapworth referred it with doubt to Dendrograptus, stating that "in its mode of branching and in its general aspect, it is a true Dendrograptus; but its thecae are quite unlike those of the typical forms of this genus, being indicated only by minute indentations, as in the genus Callograptus." They noticed however transversal corrugations or joints which might represent the thecae of Dendrograptus and therefore preferred to place the species with Dendrograptus. In the writer's specimens, the apertures appear distinctly as appressed circular indentations, without traces of projecting thecae.

### PTILOGRAPTUS Hall. 1865

Hall cited the following as the generic characters of this genus [1865, p.139]: "Frond plantlike, rooted? single or branching. Branches and branchlets plumose, the pinnules rising alternately on opposite sides of the branches; celluliferous on one face only; branches cylindrical or flattened. Substance corneous, dense; apparently smooth exteriorly, or corrugated by compression, or during fossilization."

The general habit of the types of this genus, due notably to the plumose arrangement of the branches on a principal axis, is, as Hall has first pointed out, extremely suggestive of recent hydrozoans, such as Plumularia and Aglaophenia, but this similarity is evidently only the result of convergence. Also Frech [1897] adduces these genera for comparison. The latter genus has one nematocalyx or nematophore-bearing cell in front and one on either side of each hydrotheca. It is with these defensive and prehensile individuals that Frech would compare those considered as gonangia by Wiman.

The group of forms comprised under the generic term Ptilograptus, is a very small one; for the exploitation of the rich homotaxial faunas of other countries has increased but very little the number of species described by Hall, namely by a form only doubtfully referable to this genus, described by Hopkinson from Wales. We add here a third species to the two known from the Quebec shales of Point Levis.

### **Ptilograptus plumosus** Hall

Plate 4, figure 14, 15

Ptilograptus plumosus Hall. Canadian Organic Remains, decade 2, 1865. p.140, pl.21, fig.1, 2? 3, 4

Ptilograptus plumosus Billings. Geol. Sur. of Can. Palaeozoic Fossils. 1865. 1: 366, 375

Ptilograptus plumosus Ami. Geol. Sur. of Can. Report 1889. ser. 2, v. 3, pt2, p.117k

Ptilograptus plumosus Hall. N. Y. State Cab. Nat. Hist. 20th An. Rep't. pl.4, fig.16

Ptilograptus plumosus Gurley. Jour. Geol. 1896. 4: 300

Ptilograptus plumosus F. Roemer & Frech. Lethaea palaeozoica, Bd1. 1897. p.579, fig.151

Ptilograptus plumosus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* Rhabdosome consisting of an irregularly branching principal stem and branches provided with alternately arranged closely set branch-

lets ("pinnules" Hall) which give to the colony a plumose appearance. Stem round, smooth, slightly contracted between the bases of the pinnules; .3 mm wide; total length unknown; without traces of thecal apertures in the compressed state. Branchlets slender, filiform (width about .13 mm), flexuous, closely arranged, the branchlets of one side being only .6 mm apart, forming an angle of 40° with the stem, about 3.5 mm long; showing, in the specimen here described, no thecae, but often grooves in the middle as if composed of slender tubes.

*Position and localities.* In graptolite bed 7 of the Deep kill section, which is a bed of soft shale at the dam, belonging to the zone with Diplograptus dentatus. It is also frequent in beds containing a similar congeries of fossils at Mt Moreno, near Hudson N. Y. Hall reports that the two species of Ptilograptus, which he described, were obtained in soft shale associated with Loganograptus logani, Tetragraptus quadribrachiatus, T. arcuatus, T. bigsbyi and others in the Quebec group of Point Levis. This association would indicate the zone with Tetragraptus, in which in the Deep kill section no specimens of this species have been obtained. Gurley also reports the form as only occurring in the Main Point Levis zone, and Ami observed it in material from Orleans island, with Loganograptus logani and Clonograptus rigidus. As it is very rare in the Deep kill bed, but more common in the shale of Mt Moreno, which contains a fauna transitional from a lower zone to that with Diplograptus dentatus, and in Canada is reported only from this lower zone, it would seem to have its principal development below the zone with Diplograptus dentatus. Billings found it among the graptolites from Division P at the Cowhead, Newfoundland.

*Remarks.* Hall supposed the fine transversal markings which also appear on parts of the specimen figured here, to be thecal apertures and concluded that the latter were arranged on one face of the branchlets.

### Ptilograptus geinitzianus Hall

Plate 4, figure 16

Ptilograptus geinitzianus Hall. Canadian Organic Remains, decade 2. 1865. p.140, pl.21, fig.5–8

Ptilograptus geinitzianus Gurley. Jour. Geol. 1896. 4: 300

Ptilograptus geinitzianus F. Roemer & Frech. Lethaea palaeozoica, Bd1. 1897. p.580

*Description.* This species is represented by a few somewhat fragmentary specimens which consist of a branch and the bases of the branchlets. One branch, which has a length of 21 mm, is broad (about .8 mm wide), little tapering and consisting of a thick chitinous test. The branchlets are closely alternating on opposite sides of the branch (those of the same side are 1.5 mm apart), diverge from the branch at an angle of about 50° and have a basal width of .5 mm. They are appressed to the stem for a short distance. No traces of thecal apertures are observable on them; the only indication of such an aperture being visible on the stem, near the base of a branch.

*Position and localities.* The specimens were found at the Deep kill in graptolite bed 3, the lowest bed of the zone with Didymograptus bifidus.

Hall records it as occurring in the Quebec shales at Point Levis without mentioning its associates, but Gurley observed it in the Main Point Levis zone. It seems, hence, at the Deep kill to pass beyond its range in the Quebec region.

*Remarks.* Hall's more complete specimens, which were obtained in the Quebec shale of Point Levis, show that the rhabdosome is irregularly branching. This species is said to differ from P. plumosus by its stronger and coarser habit, its more frequent and irregular branching, its broad, flattened branches and the broader branchlets. It is doubtful whether the thecal apertures are as regularly distributed on one face of the branchlets as represented in the original drawings of the species.

### Ptilograptus tenuissimus sp. nov.

Plate 4, figure 13

There has been found in graptolite bed 3 of the Deep kill section an extremely delicate rhabdosome, in fact, so tenuous that, notwithstanding its considerable length, it is only with difficulty visible to the naked eye.

*Description.* The specimen consists of a single principal stem or branch which is 28.6 mm long, but not more than .1 mm wide in its thickest part and very gradually tapering toward the distal end. The branchlets are arranged bipinnately, extremely thin (not more than .03 mm thick near their base), filiform, reaching a length of 8.2 mm. Those of one side are about 2.2 mm apart and diverge at an angle of about 40° from the stem. No traces of thecae or thecal apertures are noticeable anywhere on the branches.

*Position and localities.* Graptolite bed 3 (zone with Didymograptus bifidus) at the Deep kill.

*Remarks.* This form is easily distinguished from P. plumosus by the much longer and slenderer stem and branchlets and the greater distance between the bases of the latter, which is about four times as great as in the specimen of P. plumosus figured here and twice as great as in the type specimen of that species, which, extending to a more proximal part of the rhabdosome, has the branches a little farther apart.

This species bears some similarity to the form described by Hall as Thamnograptus anna from the same horizon, but differs by its straight, not zigzagged principal branch and the greater inclination of the branchlets.

## DICTYONEMA Hall. 1852

The generic term Dictyonema was proposed by Hall in *Palaeontology of New York*, volume 2, for a group of fossils which hitherto had been referred to such widely different groups as the gorgonias, bryozoans and the algae. It is to Hall's credit to have first observed the thecae and clearly

recognized the graptolite nature of Dictyonema in spite of its different habit [1865, p.136].

Since Hall's brief description of the genus, its characters have been repeatedly discussed, specially by Nicholson, Dames, Brögger, Tullberg and Matthew. These observers have established the fact of the presence of a sicula in several forms, as in D. flabelliforme, at the initial part of the rhabdosome, and the basketlike or conical shape of the latter, as well as the position of the thecae on the inside of the basket.

Fig.21 Dictyonema cervicorne Holm. Shows the uppermost thecae of two adjoining branches, with their forklike processes and nestlike bythecae or gonangia. x12. (Copy from Holm)

But the complicated structure of the branches was not suspected till Holm in 1890 described in D. cervicorne, from the Upper Siluric in Gotland, appendages to the thecae, shaped like birds nests [text fig.21] which he thought might possibly be gonangia. Wiman succeeded in isolating the rhabdosome and obtaining thin sections, by means of which [1895 and 1896] he has demonstrated that the branch consists of three different kinds of individuals [*see* sections, text figure 23 copied from Wiman]. These he denotes as *nourishing individuals* (his thecae, t, $t_1$, $t_2$ in sections), since they doubtless correspond to the thecae in the Graptoloidea, *budding individuals* (k, $k_1$, $k_2$ etc.) and *sexual individuals* or *gonangia* (g, $g_1$, $g_2$ etc.). The budding individuals [*see* section 6], which do not open outward, produce three individuals by gemmation, one of which is again a budding individual, while the second is a theca and the third a gonangium. All the individuals are, according to Wiman, formed in this way. Frech [1897, p.571] expresses the view that the so called gonangia of Holm and Wiman are comparable to the nematocalyces of the Hydrozoa, by adding behind gonangia (*rectius Nematophoren*).[1]

[1]Wiman has in a later paper [1900, p.188] pointed out in defense of his view that the nematocalyces occur in pairs, while but one gonangium is found associated with a theca, and further, that the nematophores, as defensive polyps, have as a rule an exposed position while the organs considered by him as gonangia are found in protected positions.

While our material, which is preserved in clay slates, seems unfit to allow any such method of investigation as Wiman employed, it will at least sometimes permit the observation of the composite nature of the branches, as in the specimen reproduced in text figure 28. In this, some parts have been slightly infiltrated with pyrite, which has brought out plastically the narrow tubes, running alongside of the thecae and presumably representing the "gonangia" and "budding individuals." The absence of any axis is also distinctly shown in this specimen. The numerous large pores appearing on the surface of certain compressed branches are apparently the apertures of the thecae.

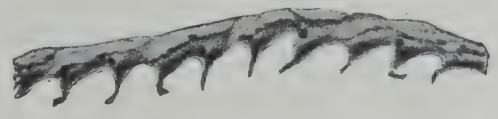

Fig.22 Dictyonema rarum Wiman. Fragment of a branch etched out of flint. Shows the thecae and the apertures of the gonangia. x11. (Copy from Wiman)

The question of the mode of life of the Dictyonemas has been mooted repeatedly. Hall gave in *Palaeontology of New York*, volume 2, plate 40, figure 1, a figure [copied 1865, p.12, fig.10], which appears to indicate a central root. This drawing has been cited frequently as proof that the rhabdosome of Dictyonema was sessile. Hall, himself, does not mention the presence of such a root in either the description of the species or the definition of the genus. He states, on page 39 of the last mentioned work, that "the Dictyonemas of the Niagara, Upper Helderberg and Hamilton groups do occur in strata which contain large numbers of other fossils, but we have no evidence of their having been attached. It is only from their general form therefore and from their analogy with other bodies, that we infer that these genera may have been attached to the sea bottom or to some objects during their growth." Nicholson [1872, p.12] doubted the presence of the root; Brögger [1882, p.32] reports that he found specimens of D. flabelliforme with siculae, the free end of which is pointed, and that "that species certainly was not attached, which in all probability may be right for the genus in general."

Matthew, who had a large collection of D. flabelliforme from the St John basin for investigation, considered it as having had a floating mode of existence [1891, 9:35]. When, later, G. van Ingen collected some specimens of the same species for him, which had short rootlets [figured 1895, pl.49, fig.1 and 2], he remarked that "it might appear from such examples as these, that it would be possible to show the existence of a sedentary variety or stage in this species; still, it does not seem that this condition of the rhabdosome is at all frequent, for among scores that have

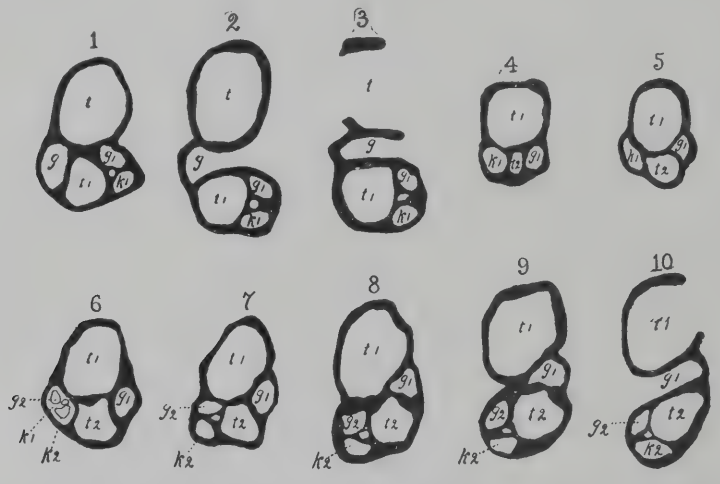


Fig.23 Dictyonema rarum Wiman. Series of thin sections. t=thecae or nourishing individuals; g=gonangia; k=budding individuals. From Lower Siluric flint-boulders of Gotland. x53. (Copy from Wiman)

been examined since these were found, none with roots have been detected." It is further suggested that these processes may have had some other office than that of anchoring the rhabdosome at the bottom, and that they are too short to afford more than a very feeble foothold at the surface of the soft ooze.

Wiman's investigations have made us well acquainted with the proximal end of at least one species, D. cavernosum. This [fig.24, 25] shows a basal disk, provided with radial ribs, which extend into a kind of network that would seem to have been well adapted to fixation on soft ooze. Wiman came indeed to the conclusion that the Dictyonemas, like all

graptolites, were denizens of the deeper littoral regions, where they formed continuous fields.

Lapworth [J. Walther, 1897, p.250] reports that in some forms of Dictyonema not only does the rhabdosome begin with a sicula, but this sicula is provided with a nema, as in the Rhabdophora, and that this nema persisted as a perpetual means of attachment to foreign bodies or to a central network of filaments (hydrorhiza) throughout the whole life of the rhabdosome.

Fig.24 Dictyonema cavernosum Wiman. Proximal end of rhabdosome, with "adhesive disk." x10 (Copy from Wiman)

All specimens of D. flabelliforme, obtained at Schaghticoke and in the region of Granville, which retained more than the sicula, showed this to extend into a fine nema [*see* the large specimen figured on pl.1, fig.20]. All the young stages, of which great numbers were obtained, possessed long nemas, often extravagantly long as in the specimen represented on the same plate, figure 1, where the nema is nearly 20 times as long as the sicula. In a few cases [pl.1, fig.10] this nema seems to end in a rather large subcircular, very thin, chitinous disk, which does not show any structural features. The nema has been slightly flexible, as its gentle curves prove, and it would appear to be hardly strong enough to have supported the young colonies, not to speak of the full grown specimens. I have, therefore, represented all these specimens as suspended.

In assuming that the rhabdosomes of D. flabelliforme were suspended, I am however well aware that there exist facts which apparently combat such a conclusion. One of these is, in my opinion, the opening of the thecae toward the inside of the basketlike rhabdosome. As the zooids were, no doubt, provided with some form of prehensile organs by which they caught small organisms, it would at first glance seem that in a suspended colony of this kind they were in a very unfavorable condition and shut out from their food supply. But it is to be considered that they may have set up, by the action of their arms, a circulation which carried organisms and food particles into the cone, where escape would be impossible; and it is also

quite likely that a suspended bell of this kind would have been voluntarily sought by numerous small animals as shelter, as some contrivances of preying water plants are sought by small crustaceans.

While, however, the specimens of D. flabelliforme from Schaghticoke are provided with thin, long nemas, Matthew has figured [1892, pl.49] two representatives of that species with short, broad rootlets. There are then three possibilities:

1 The presence of the nema in the Schaghticoke specimens and that of the short, rootlike disks in the St John specimens may constitute specific or varietal differences, indicative of an entirely different mode of existence. This seems to us very improbable, as it is not supported by any other differences observable.

2 The thin disk, observed in some young stages at the end of the nema, may grow out into the stouter disk or bundle of rootlets.

3 The adhesive disk of mature specimens may be a new formation, succeeding normally that of the nema.

In case 2 it is difficult to understand how the disk at the end of the nema could have wandered along the long nema to the proximal end of the sicula; we believe, therefore, that the disk or root of mature forms was a structure developed toward the mature age of the colony. This inference seems also to be supported by Wiman's observation, that in Discograptus schmidti, another dendroid, the bases of the branches grow directly out of this disk or are embedded in it, that hence it did not form till after the first bifurcation had taken place; and that in D. cavernosum apparently it incloses the sicula. Moreover, we have observed and will demonstrate in this paper that the "central disk" of the Dichograptidae, which is expanded between the branches, is a secondary formation, independent of the primary disk from which the nema of the sicula was suspended. It is proper to conclude that we have in the Dictyonemas a case entirely homologous to that observed in the Dichograptidae.

Lapworth appears to have made similar observations, for he states [*loc. cit.* p.253] that certain forms of Dictyonema have a short stem, others a

membrane of attachment, still others a so called disk of fixation, and others, finally, are provided with a delicate filament of attachment, which (certainly in the first growth stages of the rhabdosome) was as long and delicate as the nema of a young graptoloid. A comparison of the specimens of D. flabelliforme, from Schaghticoke [pl.1] and St Johns, shows that these different forms of attachment may even occur in the same species. Lapworth is, in the writer's opinion, therefore justified in holding [*ibid.* p.254] that, whether the nema developed into a stem, a disk, a membrane or a filament, is perhaps not so essential as it might appear at first glance, these formations all being only variations of the nema. This view is at variance with the suggestion of Holm that the basal part of Dictyonema might supply the means of a natural subdivision of the genus, which have not yet been found in the characters of the rhabdosome.

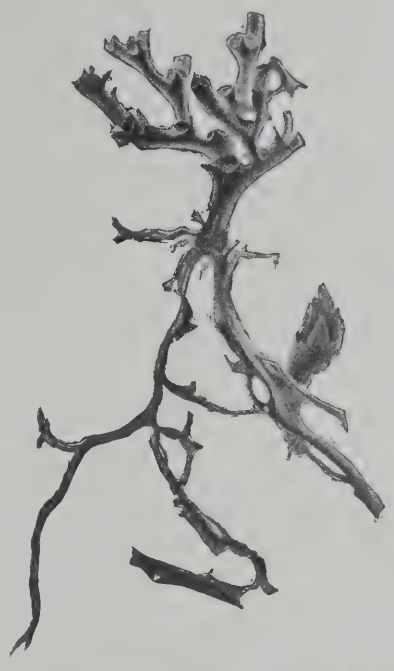

Fig. 25 Dictyonema cavernosum Wiman. Proximal end, showing stolons. x10 (Copy from Wiman)

From the appearance of the delicate, flexible nema Lapworth also concluded that Dictyonema must have been suspended like a bell at the end of a rope, as he supposes, from seaweeds.

Wiman published in 1897 [p.352] an investigation of the structure of some graptolites of Gotland. Among the latter he had a specimen of D. cavernosum which shows two colonies apparently fastened to the same stolon [*see* text fig. 25], and, as he concludes from his sections, also produced from the same hollow stolon. This discovery would, if Wiman observed correctly, introduce an entirely new mode of propagation of Dictyonema.

The question suggests itself at once, whether the long nema observed in the young of D. flabelliforme was not such a stolon. Such a view is, however, controverted by the fact that the nema begins with an adhesive

disk and ends in a distinct sicula from which the rhabdosome grows, while in D. cavernosum a stem containing a theca and a budding individual appears to grow directly from the stolon.

As Wiman has described similar stolonlike filaments as extending from the basal disks of other Dictyonemas and the rootlets of D. flabelliforme figured by Matthew are also distinctly dividing into filaments, it can be inferred that the rhabdosome of D. flabelliforme was up to maturity suspended by a thin nema from an adhesive disk [pl.1, fig.20], that it then however secured—perhaps not always—a firmer attachment by a secondary disk or a hydrorhiza, which lay close to its sicula, as is indicated by Matthew's specimens. If this disk then produced stolons from which grew new rhabdosomes, we would have rhabdosomes of two orders, those of the first order, produced directly from the sicula, and those of the second order, which budded from the stolons of those of the first order, or a composition of the entire colony somewhat analogous, but different in origin, to that found in Diplograptus.

Holm [1890, p.4f] has discussed the state of our knowledge of the genus and specially of its species and shown that most of them have been or had to be founded on insufficient material. In most cases nothing but portions of the rhabdosome have been described without knowledge of the thecae. A table given in the cited work shows that, of the 25 species known at that time, the whole rhabdosome and the thecae in their profile view were known in the case of but four. Most species are, therefore, founded only on the thickness of the branches and dissepiments, the number of branches, the form and dimensions of the meshes. He suspects, therefore, that not all forms described as Dictyonema belong to that genus, specially as it, in striking contrast to all other genera of graptolites, which are very short-lived, is the first appearing and the last disappearing genus, and thus would seem to range from the Upper Cambric into the Middle Devonic Hamilton beds. The discovery of specimens embedded in limestone will certainly furnish in time the characters necessary for a division of the genus. In fact Wiman [1900, p.189] has proposed to restrict the genus to forms

with simple branches and dissepiments (consisting of but one series of individuals) and has made a species with compound branches, originally described by him as a Dictyonema (D. tuberosum) the type of a new genus, Reticulograptus. It seems doubtful to me however whether the genus Dictyonema could be properly based on new species without regard to the original genotype, which is a Niagaran form.

It appears also that gradually the definition of the genus has been extended till it includes forms which can not be considered as falling within the scope of Hall's original definition. Therefore the subgeneric term Desmograptus was proposed by Hopkinson [1875, p.668] in recognition of the fact that in some species the meshes are not formed by parallel branches and straight dissepiments but by the coalescence of the undulating branches. Gurley argues that this group is entitled to full generic rank. As other species (Desmograptus devonicus Gurley and D. intricatus Ruedemann) are clearly proved to possess the same distinctive character, the latter will serve to establish an easily recognized division of the hitherto undivided large genus Dictyonema.

Hopkinson proposed also [*ibid.* p.667] the alteration of the name Dictyonema into Dictyograptus, on the ground that the former is an old established name for a genus of plants. This proposition has led to an interesting argument between Moberg and Törnquist [1894]. As we see no possible danger of confusion arising by the retention of the old name, we have continued to use it.

### **Dictyonema flabelliforme** Eichwald (sp.)

Plate 1, figure 1-22

Gorgonia flabelliformis Eichwald. Sil. Schicht. Syst. in Esthland. 1840. p 207
Gorgonia flabelliformis Eichwald. Urwelt Russl. H.H. 1842. p.45, tab.1, fig.6
Fenestella flabelliformis Eichwald. Beiträge z. Geol. u. Palaeont. Russl. Bul. d. l. soc. d. natur. d. Moscou. 1854. no.1, p.6; 1855. no.4, p.453
Phyllograpta sp. Ang. Pal. suec. 1854. p.4
Graptopora socialis Salter. Am. Ass'n Proc. 1857. 11:65
Dictyonema hisingeri Göppert. Üb. d. foss. Flora d. sil. dev. und unt. Kohlenform. etc. 1860. Act. Leop. 27:31, tab.36, f. 2c, 4–11; tab.45, fig.3, 4

Rhabdinopora flabelliformis Eichwald. Leth. ross. 1860. p.369

Non Dictyonema flabelliforme F. Roemer. Foss. Fauna v. Sadewitz. 1861. p.32, pl.5, fig.4 (=D. sadewitzense F. Roemer)

Dictyonema flabelliformis Törnquist. Lunds Univ. Årsskrift. 1865. t.2, III, 22, pl.1, fig.14

Dictyonema norvegicum Kjerulf. Veiviser etc. 1865. p.1, 2, fig.1–3

Dictyonema graptolithinum Kjerulf. *Ibid.* p.1, 3, fig.4, 5

Dictyonema sociale Salter. Geol. Sur. Mem. 1866. 3:331, pl.4, fig.1

Dictyonema flabelliforme Malaise. Doc. pal. rel. au Terr. Camb. de l'Ardenne. 1881

Dictyograptus flabelliformis Brögger. Die sil. Etagen 2 and 3, etc. 1882. p.30, pl.12, fig.17–19

Dictyonema flabelliforme Tullberg. Bih. till K. Svenska Vet.-Akad. Handl. 1882. Bd6, no.13. 1880–82

Dictyonema flabelliforme Schmidt. Quar. Jour. Geol. Soc. 1882. p.517

Dictyonema flabelliforme Dawson. Rep't Peter Redpath Mus. McGill Univ. 1883. p.16

Dictyonema sociale Lapworth. Roy. Soc. Can. Proc. and Trans. 1887. 4:168

Dictyonema flabelliforme Moberg. Sver. Geol. Und. Afh. och upps. 1890. ser.C, no.109, p.3

Dictyonema flabelliforme Matthew. Roy. Soc. Can. Proc. and Trans. 1892. 9:34

Dictyonema flabelliforme Wiman. Geol. Inst. Upsala. Bul. 1895. no.4, v.2, pt2, p.55, pl.10, fig.13, 14

Dictyonema flabelliforme Matthew. N. Y. Acad. Sci. Trans. 1895. 14:262, pl.49, fig.1, 2

Dictyonema flabelliforme Gurley. Jour. Geol. 1896. 4:292

Bryograptus? multiramosus Gurley. *Ibid.* p.64

Dictyonema flabelliforme Frech. Lethaea palaeozoica. 1897. 1:572, pl.2, fig.3a, 3b

Dictyonema flabelliforme Dale. U. S. Geol. Sur. 19th An. Rep't. 1899. pt3, p.185

Dictyonema flabelliforme Ruedemann. N. Y. State Paleontol. An. Rep't. 1903. p.936

*Description.* Rhabdosome a rapidly expanding cone, rate of expansion such that in the compressed state the diameter at any place is about equal to the distance of its center from the apex of the cone; cone attain-

ing a length of 5 cm and more.[1] Suspended from a thin, long nema [*see* description of genus for discussion of mode of fixation and existence of D. flabelliforme].

Branches about .4 mm wide, subparallel, rigid, bifurcating at long intervals, distant a little more than 1 mm (about 18 in 20 mm), connected by dissepiments, which are about half as thick as the branches and separated by intervals twice as wide as the latter, thus forming meshes with the branches which are about twice as long as wide. Thecae (nourishing individuals) disposed on the inside of the branches, forming short, acutely pointed or mucronate processes, numbering about 14 to 16 in 10 mm. Smaller apertures noticeable along the lateral sides of the branches.

Fig. 26 Dictyonema flabelliforme Eichwald (sp.) Fragment of branch showing lateral view of thecae and apertures of flanking tubes ("gonangia"). Schaghticoke. x5

*Position and localities.* Upper Cambric graptolite shale of Schaghticoke, Rensselaer co. N. Y., in association with Staurograptus dichotomus Emmons (=Clonograptus proximatus Matthew). Very frequent also in black slate at various localities in the slate belt in Washington county, N. Y., specially about Granville, as at North Granville, Hillsdale, on Hatch hill, on Marion hill near South Hartford, in several of which localities it is also found associated with Staurograptus dichotomus. Near South Hartford it occurs also in a dirty brownish weathering limestone. There is little doubt that its distribution extends northward through Vermont. I find for instance young specimens in a shale collected by T. N. Dale on Hamilton hill near Fair Haven in southern Vermont.

The wide distribution of this important index fossil of the closing period of the Cambric in Canada and Europe has been discussed in detail by the present writer [1903]. In Canada it has been reported by Dawson

[1] Mr van Ingen informs me that he collected, in the St John basin, specimens having a length of 10 to 12 inches.

and Lapworth from the region along the south bank of the St Lawrence from the Matane river eastward to Gaspé; further, from Cape Breton island and the St John basin by Matthew. In Europe D. flabelliforme marks the last horizon of the Cambric in Esthonia, Russia; in the black Alum shales of East and West Gothland, and of Scania; in the neighborhood of Christiania, on Bornholm; in the Lower Tremadoc of north and south Wales, and in the county Meath in Ireland; and at several localities in Belgium. This form is at once the longest known and thus far geologically oldest species of the genus and has the widest distribution of the species of Dictyonema. In distinction from the others, it appears in the horizon, characterized by it, in immense numbers, mostly to the exclusion of other forms; and the graceful suspended bells have therefore, for a short time, swarmed over a very vast tract of the northern Cambric ocean, in immense multitudes.

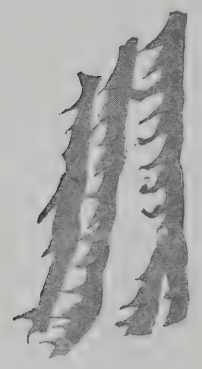

Fig. 27 Dictyonema flabelliforme Eichwald (sp.) Fragment showing dissepiment and apertures of flanking tubes. Schaghticoke. x5

*Development.* The slates at Schaghticoke have furnished a complete series of growth stages of D. flabelliforme [pl.1, fig.1–20], the first one yet made known of this genus. This permits the elucidation of a few facts.

The youngest stage observed is a relatively short and stout sicula, attached to an extremely long and slender nema [fig. 1]. By means of this nema it was probably suspended from the beginning from a subcircular, thinly chitinous organ, which is rarely observed [fig.10] and which may have been either a float or a membrane of adhesion to seaweeds etc.

When the sicula has grown beyond the length attained in figure 1; a lateral bud appears [fig.2–4] which, after a short adherence to the sicula, diverges under a very large angle (about 75°). This theca almost immediately divides [fig.5, 6] as it appears, both resulting thecae diverging about equally. Next a third theca is noticed [fig.6, 7], all three being so arranged as to form a tripod, and a fourth theca, apparently branching from the third, quickly completes the original group of four thecae

[fig.8, 9]. The formation of the four primary thecae takes place in such a narrow space — as it would appear, along a continuation of the sicula — that, where young colonies have become compressed vertically (as in figures 14 and 15) usually four branches diverge from the center. These continue to bifurcate quite rapidly, but in unequal distances [fig.15–17]. Sometimes they divide again so early that a whole bundle of branches seems to proceed directly from the distal end of the sicula [fig.16]. Where a rhabdosome, which has developed a little further, has been compressed obliquely, so as to expose the base [fig.19], one sees a central cross, each of the arms of which divides into a bush. The dissepiments or transverse connecting filaments may appear already on the branches of the second order [fig.13], but they do not become common enough to form a network till the branches of the third order have formed, as shown by figure 18.

Figures 12 and 13 demonstrate that the thecae were oriented inward from the beginning of the growth of the colony. On account of this arrangement they are very rarely noticeable, and it was possible for Dames [1873, p.383] to conclude that only the upper free ends were theciferous, a view which has been accepted in Zittel's handbook. In perfect rhabdosomes they are only occasionally noticeable in the laterally compressed marginal branches.

The early growth stages, before the appearance of the transverse dissepiments, have a considerable resemblance to those of Dichograptidae, a fact noticed by Matthews [1891, p.38]. This resemblance is indeed so striking, for instance between the early growth stages of D. flabelliforme and Clonograptus proximatus Matth., both Cambric, that, when found in the same bed, it is somewhat difficult to separate them. Matthew also states, that the first branches are formed by twice repeated bifurcation. Our material would, as we have just described, rather indicate a successive formation of the first branches, as there occur stages with one, two, three and finally with four thecae. The resemblance to the mode of branching in the Dichograptidae is hence but superficial, and can not be otherwise, since there exist fundamental differences in the composition of

the branches between the Dendroidea, including Dictyonema, and the Graptoloidea, to which the Dichograptidae belong. It also follows from the mode of formation of thecae in D. cavernosum, discovered by Wiman [1896], that the four branches of the first order should appear successively instead of in pairs; for, as the first budding individual appears together with the sicula, and produces a theca, a gonangium and another budding individual the last of which, again, gives origin to three different individuals, these thecae must, when seen exteriorly, appear in single succession and not paired; and so must the branches.

While our material does not exhibit the gonangia and budding individuals, it indicates the presence of smaller tubiform thecae also in this species, for some thecae [fig.5, 8, 9] are distinctly bipartite and tripartite, or longitudinally divided, for example the middle one in figure 8. Figure 11 represents a partly pyritized specimen, in which the composite character of the thecae becomes still more apparent.

Wiman observed, by cutting the proximal part of D. cavernosum, figured above, into thin sections, that, as soon as this part begins to show something more than the disk, there appear two individuals, namely a larger theca which opens on the stem and a smaller budding individual. By discussing the possible modes of origin of these two individuals, he arrives at the conclusion that two of them are most probable — namely, that either a free swimming, nonchitin-secreting individual became sedentary and produced the two first chitin-secreting individuals, or that the theca was older and produced the budding individual. Our series of growth stages of D. flabelliforme, presented on plate 1, tends to demonstrate the existence of a primary theca, as the inception of the colony, without any adhering tube, which could represent the budding individual [fig.1]. In regard to this theca Wiman states, that it is no common nourishing individual, i. e. no theca in the sense used for the Dendroidea; but for the latter an entirely new kind of individual, which, if not morphologically, yet functionally, as mother of but one individual, corresponds to the sicula of the Graptoloidea.

*Remarks.* The fact that the rhabdosomes of this species in the usually compressed state [fig.20] appear to be derived from a flabelliform colony, led to the early view that these organisms had been flabelliform, like gorgonias. Brögger was able to show for D. flabelliforme that its rhabdosome was actually funnel-shaped, by finding specimens where the upper and lower parts of the rhabdosome are not lying in the same bedding plane and are separated by a thin layer of shale [*loc. cit.* tab.12, fig.18]. Such specimens have been also found among the Schaghticoke material, where the upper half is partly broken away and the lower half is exposed in its place. The early growth stages, and specially such obliquely compressed specimens as those figured on plate 1, figures 16–19, leave no doubt that a cup-shaped arrangement of the branches took place from the beginning.

Brögger describes a variety of D. flabelliforme as var. confertum Linnarsson ms. and a mutation, D. flabelliforme mut. norvegicum (D. norvegicum Kjerulf). The variety confertum is said to have a much finer and closer network, and its transverse dissepiments remain always very thin. The mutation norvegicum is characterized by short angular meshes and thick dissepiments. It occurs at Vakkerö near Christiania in a higher bed than the typical form. Matthew records [1892, p.36] that the variety confertum appears to be particularly common in the lower beds at St John containing Dictyonema, and adds that it is distinguished from the typical form, found at a higher level, by its vasiform shape. The same author also refers a form which he found in the middle and upper Dictyonema bed with some doubt to D. norvegicum; and describes the principal form of St John as var. acadicum, stating that it differs from the typical Swedish D. flabelliforme by having more numerous thecae on its branches, namely 16 to 17 in 10 mm against 10 to 15 of the typical form.

As Brögger suggests it is questionable, on account of the great multiplicity of variations and transitions, whether these varieties can be kept apart. This has also been the experience of the writer with the New York material. In this, fragments bearing the characters of confertum and nor-

vegicum [pl.1, fig.21, 22] are found, which however may be only somewhat abnormal portions of, in the whole, typical specimens. The majority of the specimens are of the typical form. As the thecae usually number 15 and frequently rise to 16 within 10 mm, they would be probably referred by Matthew to his variety, acadicum.

### Dictyonema murrayi Hall

Plate 3, figure 12

Dictyonema murrayi Hall. Canadian Organic Remains, decade 2. 1863. p.138, pl.20, fig.6, 7

*Description.* Rhabdosome very large, its form unknown. Branches very stout, 1.5 mm wide, separated by slightly wider interspaces. Transverse connecting filaments straight and rigid, about 3 mm apart. Thecae numbering 9 to 10 in the space of 10 mm; apparently with acute extensions of the apertural margins.

*Position and localities.* In greenish, drab weathering sandy shales, between Defreestville and West Sandlake, Rensselaer co. N. Y. [Dale coll.]; associated with Clonograptus cf. flexilis and Tetragraptus quadribrachiatus and T. serra. These shales probably belong to the Clonograptus beds [p.496]. Hall's originals came from hard shales of the Quebec group at Point Levis, where the species is associated with other similarly robust forms of Dictyonema.

*Remarks.* The material of this species obtained at the locality mentioned, is but very fragmentary and not able to add any new data to the already meager description which Hall could furnish.

### Dictyonema furciferum sp. nov.

Plate 3, figure 11

Dictyonema sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* Portion of rhabdosome seen, flabellate; 21 mm in length by 9 mm in width; consisting of rigidly straight and parallel branches which

are not very frequently bifurcating, the resulting branches forming an acute angle; branches closely arranged, about 14 of them being counted in 10 mm; separated by interspaces of equal width with the branches. Thecae acutely dentiform, disposed on one side of the branches; numbering 16 in 10 mm; provided with a short, stout, furcate apertural process, which embraces the dorsal part of the next adjoining branch.

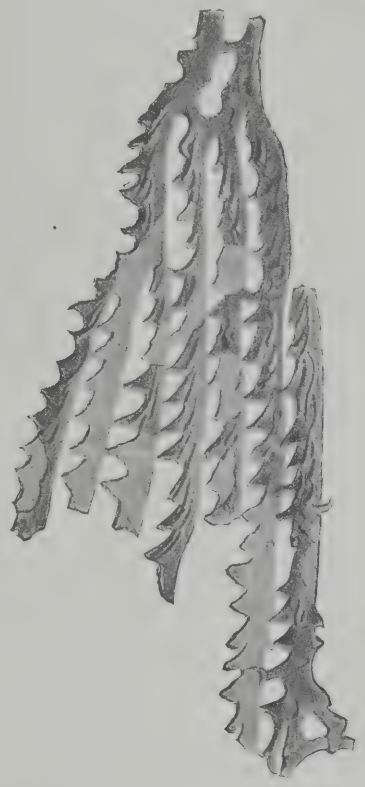

Fig. 28 Dictyonema furciferum sp. nov. The composite character of the thecae is shown by a partial infiltration of the component tubes with pyrite. Deep kill. x7

*Position and localities.* Rare at the Deep kill in graptolite bed 2 (Tetragraptus zone) and graptolite bed 3 (zone with Didymograptus bifidus).

*Remarks.* Besides small fragments and less favorably preserved branches there has been observed the single larger specimen which has been figured. This is specially noteworthy on account of the pyritization of the thecae in some parts [*see* enlarged text figure], whereby the normal juxtaposition in the branch of several (apparently three) slender tubes becomes apparent.

The character of the dissepiments, which are prolongations of the thecae ending in furcate processes connects this species with D. cavernosum and peltatum Wiman, from the Lower Siluric of Gotland, and with D. cervicorne Holm, from the Upper Siluric of Gotland.

### **Dictyonema rectilineatum** sp. nov.

Plate 3, figure 10

cf. Dictyonema delicatulum Dawson. Can. Nat. and Geol. 1883. 10:461f
Dictyonema sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* Form of entire rhabdosome not known. Branches at proximal end forming an irregular mesh work; in a more distal zone radiat-

ing and bifurcating rapidly; in the greater part of the rhabdosome rigid, nearly straight, very closely arranged (about 12 to 14 in 10 mm) and extraordinarily regularly parallel. Width of branches .4 mm. Interspaces from one to one and a half times as wide as the branches. Dissepiments very slender, not exceeding .16 mm in width; mostly straight, a little more distant than the branches (about 1 mm); the resulting meshes hence shortly rectangular. Branches dividing at an acute angle. Thecae not observed. Apertures apparently irregularly disposed, larger ones, approximately corresponding in number and position to the dissepiments, separated by more numerous smaller apertures.

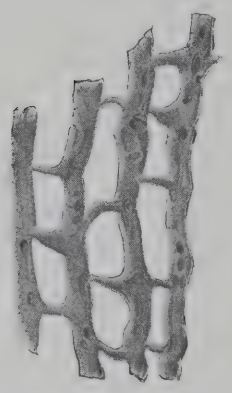

Fig. 29 Dictyonema rectilineatum sp. nov. Enlargement of part of the specimen reproduced on plate 3, figure 10. Deep kill. x9

*Position and localities.* Rare in the horizon with Diplograptus dentatus and Climacograptus? antennarius at the Deep kill.

*Remarks.* This form is evidently closely related if not identical with the species described by Dawson as D. delicatulum, which name, being preoccupied by a species name given by Lapworth, was changed by Gurley into D. perexile. However, as Dawson did not furnish any drawings, his short description does not allow any positive identification, and, moreover, as his form has still more closely arranged branches (18 in 10 mm) and occurs in another association of species (Phyllograptus typus, Tetragraptus bryonoides and T. bigsbyi), it was not thought safe to identify the form described here with his species. Ami has listed [1888, p.117k] a form doubtfully referred to Dawson's species, which he cites, in recognition of the fact that its name was preoccupied, as Dictyograptus *n. sp.* and records as occurring at the road from Levis to St Joseph with Didymograptus bifidus, D. extensus, D. furcillatus, D. pennatulus, Tetragraptus approximatus, T. fruticosus, T. quadribrachiatus and T. serra, and Phyllograptus typus, an association which distinctly points to the next older horizon than that in which our form is found at the Deep kill;

and as also occurring at the Cliff facing the foundry at Levis, associated there with the common species of Tetragraptus and Diplograptus dentatus, an association which would indicate a transitional bed between the horizons of Didymograptus bifidus and Diplograptus dentatus.

### DESMOGRAPTUS Hopkinson

The name Desmograptus was proposed by Hopkinson [1875, p.668] as a subgeneric term of Dictyonema for forms in which, as in the genotype, D. cancellatus, "the meshes or interspaces are chiefly formed by the branches coalescing and dividing by virtue of their curvilinear direction." The flexuous and anastomosing course of the branches forms a character so readily recognized and so distinctive of a group of species, that we have no hesitation in recognizing the latter as a genus. This is represented in the Deep kill fauna by two species.

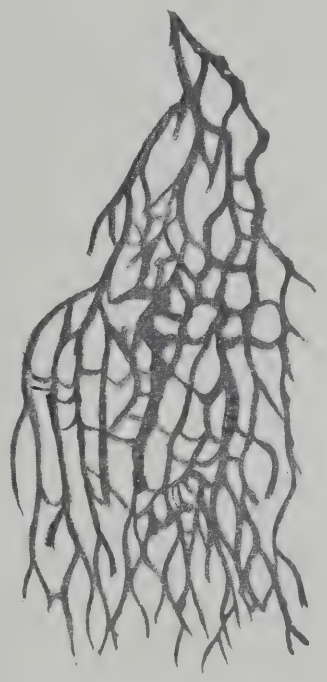

Fig. 30 Desmograptus intricatus sp. nov. Enlargement of proximal portion showing transition from straight to undulating branches in lower part. Deep kill. x5.25

The presence of occasional dissepiments and of parts with more straightened branches in D. intricatus suggests, however, that the structural differences between Dictyonema and Desmograptus may not be as great as it would appear from their widely different aspects. Of special interest in regard to this relationship is the basal part of the specimen, reproduced in figure 30, which shows in the oldest proximal part parallel branches and true, stout dissepiments. This Dictyonema structure rather abruptly changes into the Desmograptus structure with irregular and coalescing branches, a change which indicates the development of Desmograptus from the typical, also geologically older Dictyonema.

### Desmograptus cancellatus Hopk. (sp.)

Plate 3, figures 5–8

Dictyograptus (Desmograptus) cancellatus Hopkinson. Quar. Jour. Geol. Soc. 1875. 31:668, pl.36, fig.11a, 11b

cf. Desmograptus macrodictyum Gurley. Jour. Geol. 1896. 4:83f

Dictyonema (Desmograptus) cancellatum Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* Rhabdosome infundibuliform, beginning with a chitinous, apparently nonsiculate basal expansion, and a short stem. Branches thick, undulating, in the proximal part little flexuous and subparallel, distally becoming gradually more undulating; forming by coalescence and redivision in the proximal parts long narrow meshes; in the distal parts elongate to broadly oval meshes. These are in the mature parts about twice as wide as the branches and three to four times as long as wide. Branches 12 to 14 in 10 mm. Thecal apertures circular, not prominent, appressed to branches, apparently closely arranged. Dissepiments rarely observable. Bifurcation of branches quite regular, leading to a regular gradual expansion of the rhabdosome.

Fig. 31 Desmograptus cancellatus Hopkinson (sp.) Enlargement of part of specimen reproduced on plate 3, figure 7. Deep kill. x3.75

*Position and localities.* Common in graptolite bed 7 of the Deep kill section (horizon with Diplograptus dentatus and Climacograptus? antennarius).

D. cancellatus was described as coming from the Lower Arenig of Whitesand bay of St David's, which is stated to be overlain by Middle Arenig beds containing some of Hall's species of Tetragraptus, Callograptus and Didymograptus, occurring here in the Tetragraptus beds. It would, therefore, seem that the British species is considerably older than the Deep kill form, referred to it. As, however, Trigonograptus ensiformis, a typical species of the third Deep kill horizon, in which D. cancellatus occurs, is cited as having been found in the Lower Arenig of Whitesand bay, it is possible that at the latter locality the beds are inverted or

otherwise disturbed, and the terms Lower and Middle Arenig should be exchanged.

If, however, the species recorded by Gurley from the Main Point Levis zone which corresponds to the Tetragraptus beds of the Deep kill section is identical with our form, the latter would range from the Tetragraptus horizon to that with Diplograptus dentatus.

*Remarks.* This form, in some of its distal parts, agrees so closely with the description and figure of Dictyograptus (Desmograptus) cancellatus, that a separation from this species does not appear to be justified. The only apparent difference is the greater width of the branches in the Welsh specimen, a feature which in view of the variability of the thickness of the branches in the Deep kill specimens can not be considered as of diagnostic value. The figure of the type specimen which is a representation of a more distal part shows also the presence of more elongate meshes in a basal direction.

Fig. 32 Desmograptus intricatus sp. nov. Enlargement of part of the specimen reproduced on pl.3, fig.3. Deep kill. x6

Gurley described a form from the Beekmantown shales of Point Levis as D. macrodictyum, which is said to differ from D. cancellatus by the straight branches, the greatly elongate meshes and the generally stouter structure. As the specimens figured here exhibit these same differences between basal and distal parts of the rhabdosome, it is probable that his type is also referable to this species and belongs only to a more basal portion than the original. Since Dr Gurley did not figure his species, which was found in the Main Point Levis zone, a definite reference is excluded at present.

### Desmograptus intricatus sp. nov.

Plate 3, figures 1–4

Dictyonema (Desmograptus) sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* Rhabdosome infundibuliform; rapidly widening by oft repeated bifurcations of the branches, attaining a length and width of

50 mm. Branches thin (.1 mm), very closely arranged, numbering 16 to 20 in 10 mm, subparallel, undulating and coalescing at the contact points, forming elongate meshes, eight of which have a length of 10 mm. True dissepiments occurring but rarely. Thecal apertures not prominent, appressed, appearing as closely arranged circular pores.

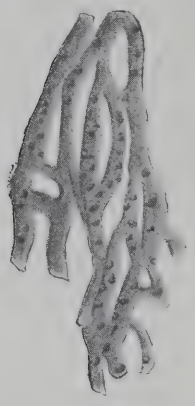

Fig. 33 Desmograptus intricatus. Enlargement of portion of the specimen reproduced on pl.3, fig.1. x8

*Position and localities.* Very common in graptolite bed 7 of the Deep kill section, belonging to the horizon with Diplograptus dentatus.

*Remarks.* This species is readily distinguished by the delicacy of its structure and the small size of its meshes from D. cancellatus, which occurs in the same bed, and by the undulating character of its branches from Dictyonema rectilineatum, a similarly fine meshed form of the same horizon.

## Order 2 GRAPTOLOIDEA Lapworth

## Suborder A GRAPTOLOIDEA AXONOLIPA Frech, em. Rued.

## Family DICHOGRAPTIDAE auct. em. Frech

### STAUROGRAPTUS Emmons

(=Clematograptus Hopkinson and Clonograptus Hall in part)

Emmons proposed, in the second part of his *American Geology* [1855, p.108] the new genus Staurograptus for a minute form, which he had found in the "Taconic shales of Rensselaer county, N. Y." His definition of the genus is: "Disk free, cruciform, arms four, dichotomous cells terminal, substance membranaceous, free and furnished with an axis." This genus has, on account of the peculiar aspect, the cruciform division in the center and the peculiarly broad dichotomous appendages [*see* Emmons's two drawings, reproduced here] of the genotype, S. dichotomus, been considered as doubtful at the beginning and later suffered still worse fate, for it has in all newer works on graptolites been delivered to complete oblivion.

The only note on the genus, which is known to me, is that by Hall [1865, p.43] which reads: "The typical and only species of Staurograptus of the same author is a very remarkable form of extremely minute proportions. Its mode of growth and subdivision of stipes, if accurately represented in the figure, are unlike anything known among this family of fossils, and it merits generic distinction." Lapworth refers to it [1887, p.168] as the "dubious genus Staurograptus of Emmons."

I have now found in the same region whence Emmons obtained this material, in slates associated with the Upper Cambric Dictyonema flabelliforme bed, a complete series of growth stages [pl.2] leading from the sicula through stages identical with Emmons's Staurograptus dichotomus to Clonograptus proximatus, a species described by Matthew from the Upper Cambric of the St John basin. Though the mature specimens of the species look very different from the growth stage which Emmons happened to have, the right of priority requires, I think, the recognition of his generic and specific terms.

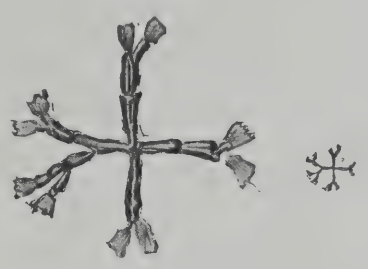

Fig. 34 Staurograptus dichotomus Emmons. Copy of original figures

It is evident from Emmons's description that he considered his specimen as full grown, and as having normally "dichotomous cells terminal," but this does not vitiate the fact of his recognizing the differential character of this form, consisting in the cruciform center.

The recognition of the generic term Staurograptus would make Hall's term Clonograptus a void synonym, in case the mature form here described should be referable to the latter genus. It is however certain that the form presents, in its mature stage, characters of Hopkinson's genus Clematograptus [1875, p.652]. The latter is characterized in its type species, Cl. implicatus Hopk., by the radial disposition of its branches, which branch so closely to the sicula that they all appear to spring at once from the center, and that the "funicle" of other Dichograptidae is hardly noticeable. This concentration of branching of the rhabdosome in the early

stages, causing a bushlike mode of branching [pl.2, fig.13, 14, 16] is the only difference which the writer can find between Clonograptus and Clematograptus, and it is quite probable that this is of no more than subgeneric importance. As, however, the latter genus has been commonly recognized and comprises a small group of forms which is well characterized by the feature mentioned, we will distinguish it here also though under the older term Staurograptus.

### Staurograptus dichotomus Emmons

Plate 2, figure 1-24

Staurograptus dichotomus Emmons. Am. Geol. pt2. 1855. p.109, pl.1, fig 21

cf. Bryograptus patens Matthew. Roy. Soc. Can. Trans. and Proc. 1893. v.10, §4, p.17, pl.7, fig.1a, 1c, 1d

Clonograptus proximatus Matthew. N. Y. Acad. Sci. Trans. 1895. 14:265, pl.48, fig.1a-d

cf. Bryograptus patens Matthew. N. Y. Acad. Sci. Trans. 1895. 14:268, pl.48, fig.4a, 4b[1]

cf. Bryograptus lentus Matthew. N. Y. Acad. Sci. Trans. 1895. 14:270, pl.48, fig.2a, 2b

Clonograptus proximatus Ruedemann. N. Y. State Paleontol. An. Rep't. 1903. p.938

Bryograptus patens Ruedemann. *Ibid.* 1903. p.938

Bryograptus lentus Ruedemann. *Ibid.* 1903. p.938

*Description.* Rhabdosome broadly conical to saucer shaped; mostly found vertically compressed or spread out. Sicula short (about 1.8 mm long) and slender conical, suspended by means of a delicate nema, which attains four times the length of the sicula and has not been observed in grown specimens, from a chitinous disk that in diameter approximately equals the length of the sicula [pl.2, fig.1]. Primary thecae ("funicle") growing in direction of the sicula, rhabdosome hence apparently beginning with four or more branches. Rhabdosome attaining a diameter of 40 mm, consisting of numerous (upward of 40) branches of the last order. Branches slender

[1] Figure 4c appears to me to represent an early growth stage of Dictyonema flabelliforme

(about .4 mm wide in the dorsal aspect and .6 mm in the lateral aspect), straight in the central parts and slightly flexuous in the distal region, branching dichotomously in irregular intervals. Branches of six orders observed; the bifurcation of the first branches takes place under right angles, those of succeeding orders under angles of 50°-70°, the angles of bifurcation decreasing distally. The thecae number 11-13 in 10 mm; they are inclined at a constant angle of 25°, and are in contact for a little more than one third of their length; their outer walls are straight or slightly concave, the apertural margin gently convex and nearly vertical on the axis.

*Position and localities.* Common in the Upper Cambric slates at Schaghticoke N. Y. It occurs undoubtedly at other places in the slate belt, in Rensselaer and Washington counties, in association with Dictyonema flabelliforme. It is, for instance, very common in Upper Cambric slates from Hillsdale near Granville, Washington co. Emmons obtained his types from the Taconic slates of Rensselaer county, N. Y. Matthew records the species as occurring in bands of division 3 of the St John group, where it is also associated with D. flabelliforme.

*Development.* This species has furnished a complete series of growth stages. These begin with (1) the sicula [pl.2, fig.1, 2], which is suspended by a rather short nema from a thin chitinous disk; (2) the sicula produces at about one third of its final length the first theca [fig.3], which grows appressed to the sicula nearly as far as the latter's aperture and thence turns to the left [fig.4, 5, 6]; (3) from the first theca originates at about one fourth of its length [fig.4] the second theca, which also grows along the sicula to the point of departure of the first theca and then turns to the right side. The "funicle" of other dichograptids, which is composed of these two thecae, is, hence, here not noticeable in a horizontally spread out colony. (4) Both primary thecae produce by budding in rapid succession two apparently dichotomous branchings [fig.6] close to the aperture of the sicula; thus giving origin to the cruciform division in the center of the

colony, when seen in a vertically compressed condition [fig.8-10]. The cross of branches stood vertically on the axis of the sicula or had a horizontal position in the suspended rhabdosome as is illustrated by figures 7 and 17. (5) The four branches of the second order form at once new bifurcations. One of them lies usually a little closer to the center [fig.9-11] than the others, thus often giving to the colony the appearance of having possessed a six rayed center [fig.12-14]. The stage with the four branches of the second order and the eight branches of the third is that which Emmons figured and employed to base his S. dichotomus on. (6) The later branches bifurcate irregularly and apparently, as in Clonograptus, without limitation. (7) The laterally compressed specimens [fig.17-21] show that the branches at the beginning grew in a nearly horizontal direction [fig.17,19], but later on turned obliquely downward, the whole rhabdosome thus forming an inverted broad, low cone [fig.20,21] with an apical angle of 110°-120°.

*Remarks.* Where the initial branching is not very distinct, a criterion by which the last mentioned laterally compressed forms could be distinguished from species of Bryograptus is lacking; and without the presence of the other flat mode of preservation and the growth stages they could hardly help being considered as belonging to that genus. It is evidently for these reasons that Matthew [1895] has described two species of Bryograptus as associates of the species under discussion, which, from the extensive material collected at Schaghticoke, I believe to be other modes of preservation of S. dichotomus. In a preliminary paper on the Dictyonema flabelliforme beds in New York [1903, p.938] the writer has also listed these species of Bryograptus which he at first thought to be well distinguished from Staurograptus.

While, however, the Bryograptuslike mode of preservation is by far the rarer — as is also stated by Matthew — both the normal Staurograptus and the Bryograptus form have been noticed in the same specimen, one part of which had been flattened vertically and another compressed laterally. This supports the suggestion of Elles [1898, p.532] that "great variation

might be observed in a delicate Clonograptus form in the angles at which the stipes of various orders were inclined to each other." For, if we consider the rhabdosome to have been free floating or attached to some floating body, and its branches as flexuous, it is obvious that the latter might ultimately come to rest in quite different positions.

### **Staurograptus dichotomus** var. **apertus** var. nov.

Plate 2, figures 22-24

There have been found in the Upper Cambric beds of Schaghticoke and of Hillsdale near Granville, specimens of S. dichotomus which contrast with the great majority of the individuals by their greatly reduced bifurcation and a correspondingly much smaller number of branches. The latter appear, in the extreme cases, as the original of figure 22, to have but branches of the first two orders. There are no differences observable in the character of the thecae and transitional forms, as the one reproduced in figure 23 demonstrates the close connection of these forms with the types of the species.

This variety bears some similarity to Graptolithus milesi Hall [Geol. Vt. 1861, 1:372, figured v. 2; 1861, pl.12, fig.2-4] in the mode of its branching and the character and number of its thecae. It has in the preliminary paper cited above [1903, p.938] been referred provisionally to that species. A direct identification is prohibited by the statement of the presence of a horizontal "funicle" in G. milesi, which species then is to be referred to Clonograptus[1].

[1]This species has been referred by Nicholson [1876, p.248] to his new genus Temnograptus. Herrmann did not recognize that genus [1886, p.25] and referred its species to Clonograptus; while Frech [1897, p.596] follows Nicholson, and refers both species, Temnograptus milesi and T. multiplex, to Temnograptus, suggesting that they may be identical. A comparison of the drawings of Clonograptus milesi with those furnished of Temnograptus multiplex by Nicholson [*op. cit.*] and Elles [*op. cit.* p.479, fig.6] leaves however no doubt that in the former species the branching is typically dichotomous, while in Temnograptus it is monopodial or lateral, notwithstanding the fact that Nicholson and Elles cite the wholly

### CLONOGRAPTUS Hall. 1873

#### Clonograptus cf. flexilis Hall

Graptolithus flexilis Hall. Geol. Sur. Can. Rep't for 1857. 1858. p.119
Graptolithus flexilis Hall. Canadian Organic Remains, decade 2. 1863. p.103, pl.10, fig.3-9

Only fragments of a form, not sufficient for definite determination, but probably belonging to this species, have been collected by T. N. Dale at a locality between Defreestville and West Sandlake, Rensselaer co. N. Y.

### TEMNOGRAPTUS Nicholson

Fragments of a very coarse and massive graptolite [pl.5, fig.15–20] demonstrate the presence in the Deep kill beds of a single representative of a peculiar group of multiramous types of truly gigantic dimensions when measured by the average graptolites. Some rhabdosomes of this group of forms covered an area of 1 qm and more. The whole aggregation which is typically represented by the genus Temnograptus, and to which, besides, belong the genera Schizograptus, Trochograptus, Holograptus and Rouvilligraptus, is characterized by the large size of the multiramous rhabdosomes, the mostly considerable thickness of the branches, the widely and equally separated points of branching and the strong development of the lateral branching. All these features give to the group a uniform habit quite distinct from that of the other graptolites.

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dichotomous branching as one of the distinctive characters of Temnograptus. That in T. multiplex the branching is indeed monopodial becomes evident in Nicholson's and Elles's drawings, which show that one of the branches resulting from the division follows the curvature of the mother branch, while the other alone assumes a new direction. Only the branches of the first order divide dichotomously; and it is hence probable that no difference can be found between this and Holm's genus Trochograptus, as according to Elles's table [p.478] the mode of branching constitutes the only difference between the two.

We believe, for these reasons, that Clonograptus milesi and Temnograptus multiplex belong to quite different series of the dichograptids.

Of the above named genera, Temnograptus shows still in its branching the nearest approach to the original dichotomy, the others possessing mostly a more distinctly lateral mode of branching, and it also has still the greatest number of orders of branches; hence it seems to be nearest to the ancestral Clonograptus forms, and therefore may have been the radicle of the others.

In the American graptolite beds this group, which in Europe is well developed, is but poorly represented. A single other species besides the form here described has become known, viz Holograptus richardsoni, from the Quebec beds.

### Temnograptus noveboracensis sp. nov.

Plate 5, figures 15-20

Temnograptus cf. multiplex (Nicholson) Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556.

In graptolite bed 2, representing the upper part of the Tetragraptus shale, frequently occur fragments of a large branching dichograptid of strikingly different habit from the associated forms. As no entire specimen has been observed, the structure of the rhabdosome could be obtained only by a combination of fragments. This proves the form in question to have possessed a short stout "funicle," from which branched by dichotomy four long denticulate secondary branches, which in long intervals bifurcated again. There were branches of at least four orders.

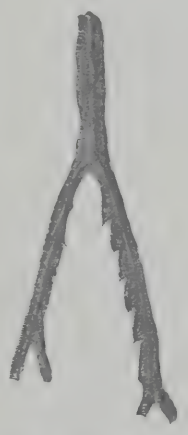

Fig. 35 Temnograptus noveboracensis sp. nov. Fragment of rhabdosome showing bifurcations and form of thecae. Deep kill. x4.5

*Description.* Branches of first order short (5.5 mm), stout; those of the second and following orders long (50+mm), forming an angle of 130°. Branches of the higher orders bifurcating under smaller angles, the latter apparently diminishing with the increasing distance from the base of the rhabdosome. Angles of 70°, 30° and 10° have been measured in various

branches. Bifurcations very far apart, longest branch 215 mm, maximal width of branch (much flattened out) 2.4 mm. Thecae numbering, apparently, 10 in 10 mm, little prominent, inclined at a low angle (about 10°).

Fig. 36 Temnograptus noveboracensis sp. nov. Fragment of a slightly obliquely compressed branch. Dorsal view showing the internal apertures of the thecae. Deep kill. x3

*Position and locality.* Graptolite bed 2 (Tetragraptus horizon) of the Deep kill section.

*Remarks.* This species, which is the only representative of the entire group in the Deep kill beds, is distinguished from the type species of the genus, Temnograptus multiplex, by the straight direction and more rigid appearance of the branches and the smaller angles of divergence of the branches and of inclination of the thecae. From Hologra ptus richardsoni Hall (sp.), its only closer American relative, it differs by its much more widely separated points of bifurcation, more nearly dichotomous branching and smaller angle of inclination of the thecae.

### GONIOGRAPTUS McCoy. 1877

The genus Goniograptus was proposed by McCoy [1876, p.128] for "such types as the present, in which the branches of the funicle (for which I would suggest the name stolons) are regularly bent at the points of budding into the celluliferous stems." The genus was recognized by Lapworth, while Roemer and Frech, from the point of view that the mode of branching is of little generic importance in comparison with that of the form of the thecae, are inclined to refer Goniograptus to Clonograptus, which is retained as a subgenus of Dichograptus.

While in Clonograptus the branching takes place entirely irregularly and thus represents a primitive stage of development, it has become rigidly fixed in Goniograptus in such a fashion that four zigzagged principal axes are formed, from the angles of which regularly spring undivided branches. The peculiar direction of development taken by this species appears

not to have been fruitful of further forms, like the main stem of the Clonograptus forms, and the small branch became soon extinct. There have been found two more forms in the Deep kill beds with the same rigid Goniograptus structure, but thecae of different dimensions. These forms show that there exists a whole group presenting these characters of structure different from those of Clonograptus and requiring recognition. But their different thecae leave also little doubt that the genus is polyphyletic [ch.10, p.561]. The name then still would designate a definite phyletic stage or tendency of development which it seems became manifest only in the Pacific-American basin [p.503].

### Goniograptus thureaui McCoy

Plate 6, figures 1-15

Didymograptus (Goniograptus) thureaui McCoy. Ann. and Mag. Nat. Hist. ser. 4. 1876. 18:128-130

Graptolites (Didymograptus) thureaui McCoy. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 5. 1877. p.39, 40

Goniograptus thureaui var. selwyni Ami. Can. Record Sci. 1889. 3:422-28, p.502, 503, fig.1, 2

Goniograptus thureaui Ami. Geol. Sur. Can. Rep't. ser. 2. 1889. v.3, pt 2, p.116k

Dichograptus (Clonograptus, Goniograptus) thureaui Frech. Lethaea palaeozoica, Bd 1, Lief. 3. 1897. p.600, fig.165

Goniograptus thureaui Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556, 565, 576-92

Among the many pretty patterns of graptolite structure occurring in the zones with Tetragraptus and Didymograptus bifidus undoubtedly the most beautiful is G. thureaui McCoy. Our interest in this form is enhanced by its peculiar distribution and the fact that it has left a complete record of its ontogeny [1902, p.576].

The form was first made known by McCoy from the black and red auriferous slates of the Bendigo gold field, at Sandhurst, Victoria, Australia, and the new genus Goniograptus based on the same. In 1889 Dr Ami announced the discovery of this remarkable graptolite in the

Tetragraptus shale of the Levis beds in Canada, noting in a description of the same the presence of a central disk which had not been observed in Australia.

*Description.* The rhabdosome consists of two short monothecal branches of the first order ("funicle") growing from a relatively long, stout sicula (2.2–2.7 mm in different specimens). The "funicle" varies from 2.3 to 3mm in length. It divides by dichotomy at both ends into two short branches of the second order which form an angle varying between 130° and 140°. These bifurcate again, forming two branches, one of which grows out into an undivided denticulate branch, while the other monothecal one bifurcates, producing a denticulate branch on the opposite side. This process is repeated till four zigzag shaped, principal stems are formed, reaching a length of 10 mm and lying approximately in the diagonals of a rectangle, forming two pairs of angles, the one at the end of the "funicle" being about 75°, the other on both sides of the same 105°. The denticulate branch forms an angle of 45° with the stem and the last pair of succeeding denticulate branches form approximately a right angle at their bases. The whole rhabdosome expands in the form of a square with convex sides.

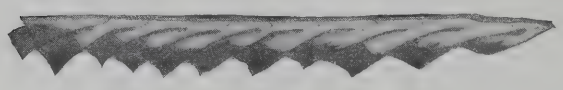

Fig. 37 Goniograptus thureaui McCoy. Fragment of a branch in which the coenosarcal canal and the proximal portions of the thecae have become infiltrated with pyrite and the successive gemmation of the thecae is well shown. Deep kill. x5.25

Fig. 38 Goniograptus thureaui McCoy. Fragment of branch enlarged. Deep kill. x4.5

Well preserved, mature specimens often possess a chitinous disk which clasps the "funicle" and the principal branches to the base of the terminal denticulate branches. The breadth of this alate extension has not been found to surpass 1.3 mm. The diameter of the largest colonies was observed to be 110 mm. The thecae are long and narrow, number 8 to 10 in 10 mm, overlap about one half of their length; their outer walls are slightly concave and are inclined at about 30° to the axis of the branch in the distal parts; their

apertural margins are also concave and form an angle of 80° with the axis of the branch.

*Position and localities.* G. thureaui is common in graptolite bed 2 (Tetragraptus zone), but extends apparently in diminished size and development, into the next zone, that with Didymograptus bifidus. In Canada it is according to Ami's lists restricted to one locality at Levis, where it is associated with the Tetragraptus fauna. McCoy recorded the originals as occurring in the "Llandeilo" of the Bendigo gold field of Australia. It is however certain that it there also occurs at about the same horizon in rocks of Arenig age. The significance of the distribution of this form for the reconstruction of the paleozoic marine basins has been discussed in the chapter on the range and distribution of the graptolites [p.503].

*Remarks.* The dimensions and angles, as well as the general structure of the Deep kill specimens, agree closely with those given in the descriptions of the Australian and Canadian types, leaving no doubt of the specific identity of the forms. At the same time the Australian specimens are reported to have 40 branches, the Canadian types even attain as many as 80, while none from the Deep kill have been observed to have developed, even in large specimens, more than 24, or six on each stem. Though the fact is now well established that, in the multiramous dichograptids, the number of branches furnishes no criterion for generic distinctions, it is also proved that in the phylogeny of this group there can be recognized a tendency to reduce the number of branches and to attain a fixed, though restricted number. In this process the Deep kill forms seem to have reached a stage beyond that of the more multiramous Canadian and Australian forms. The writer proposed in a former paper [1902, p.580] to designate this stage by the varietal name postremus.

In the paper mentioned it has been demonstrated by means of the numerous growth stages of this species found at the Deep kill, which furnish an unbroken series [pl.6, fig.1–10 of this memoir], that the "funicle" consists of two thecae, formed by dichotomous branching from the sicula,

and that also the stem internodes between two bifurcations consist of but one theca each; that hence the entire rhabdosome from the sicula on is built up of thecae; and that there are no indenticulate branches. There exist however morphologic and functional differences between the earliest thecae, which are constituent parts of the stems and the later thecae of the branches, differences which also appear within the denticulate branches themselves. These differences were held to indicate ontogenetic stages of the nature of those which have been termed "localized ontogenetic growth stages" by Jackson. Here the localization appears in so far as each branch passes in the shape and arrangement of its thecae, like an organ of the whole rhabdosome, through ontogenetic stages, indicative of phylogenetic or evolutionary stages passed by the species.

A single specimen [pl.6, fig.14] was obtained which had not been spread out like the others on the bottom of the sea, but became compressed laterally. This shows that all branches were held in a nearly horizontal position, curving slightly upward in the distal parts[1]; and that the thecae pointed all in one direction, viz downward, assuming the suspended position of the rhabdosome. Another specimen has been figured here because it exhibits an abnormal irregular branching on one (left) side [pl.6, fig.15].

Fragments of rhabdosomes which have been stripped of a part of their branches, are liable to assume very misleading aspects. Specially numerous were specimens retaining only four branches, in such a manner as to suggest a Tetragraptus [pl.6, fig.13]. These, then, in the character of their branches and thecae, are somewhat similar to Tetragraptus hicksii Hopk. & Lap. [1875, p.651], a species which has lately been recognized to be based on a bundle of rhabdosomes of an Azygograptus.

[1] The drawing has been inverted by mistake.

### Goniograptus perflexilis sp. nov.

Plate 6, figures 16-18; plate 7, figures 1-9

Goniograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556

In the two lowest graptolite horizons of the Deep kill section occur two closely allied species of very delicate multiramous dichograptids which unite the mode of branching characteristic of Goniograptus with the diverging of the primary thecae from a point close to the apical end of the sicula, peculiar to the coenograptids. The type occurring in the Tetragraptus horizon is the one described here.

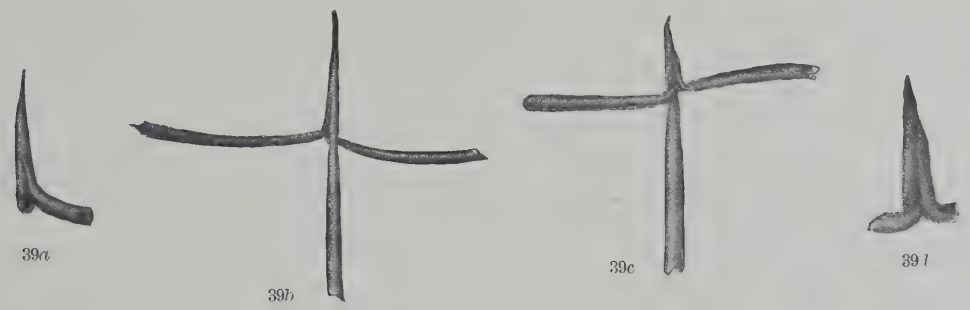


Fig. 39 Goniograptus perflexilis sp. nov.: *a* Sicula and first theca. 7x; *b* Growth stage of rhabdosome with two first thecae. Obverse view. x7; *c* Similar stage. Reverse view. x7; *d* Further enlargement of proximal parts of first two thecae. x21. Deep kill

*Description.* Sicula extremely long and slender (4 mm long and but .3 mm wide), the first thecae originating close to the apical point of the sicula [fig.39], and adhering to the latter for a very short distance and then producing a second theca; both first and second thecae diverging from the sicula at right angles; these thecae but little shorter than the sicula and equally narrow, straight or slightly curved, with the convex side directed downward; each of these thecae producing again two thecae, which together form an angle of 80°. The resulting thecae form the bases of the four principal stems, which, hence, diverge at an angle of 80° and which, as in the type species of the genus, give off undivided branches alternately on opposite sides from the outer points of the angles of their zigzag shaped course. The stem divisions form an angle of 160° with each

other; the branches leave the stems with an angle of about 80°. The branches are extremely slender, their maximal width observed being only .4 mm. The total length attained by the branches and the diameter of the whole rhabdosome are not known. Six branches have been observed on principal stems which were not perfect. The thecae are extremely narrow, long and tubular, 3 mm long, increasing to 5 mm in the distal stem sections; in the mature branches about six times as long as wide; in contact more than one half of their length, numbering not more than 6 to 7 in 10 mm, and forming an angle of but 5° with the axis of the branch. They have gently concave outer margins, nearly straight, reflexed apertural margins, which form an angle of 60° with the axis of the branch.

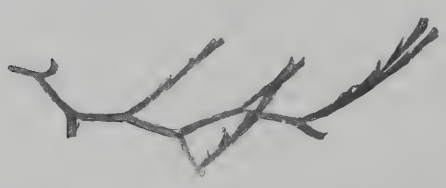

Fig. 40 Goniograptus perflexilis sp. nov. Enlargement of a part of the specimen reproduced on plate 7, figure 9, to show the composition of the steminternodes of thecae and the character of the thecae. Deep kill. x2.5

*Position and localities.* In graptolite bed 2, forming the upper part of the Tetragraptus horizon in the Deep kill section, and rarely also in the next horizon. While younger growth stages were found very frequently, mature colonies are extremely rare in this material. One large fragment referable to this species [pl.6, fig.16] was obtained from the beds at Mt Moreno near Hudson which are transitional from the horizon with Didymograptus bifidus to that with Diplograptus dentatus, so that this species ranges from the second to the lower part, at least, of the fourth horizon.

Fig. 41 Goniograptus perflexilis sp. nov. Enlargement of branch of the specimen reproduced on plate 6, figure 17. Deep kill. x5.25

*Remarks.* This species is at once distinguished from G. thureaui by its extremely slender habit, the narrow branches and longer thecae, the less angular nature of the principal stems, which more approach to a straight line. In the location of the budding and diverging points of the thecae, forming the "funicle" it differs markedly from the type species of the genus

and all other multiramous dichograptids known to the writer, in having these points close to the apical end of the long sicula. It has been noted in the chapter on the phylogeny of the dichograptids [p.561] that this is one of a number of characters which indicate a connection of this species with a separate phylogenetic series of forms, ending in the coenograptids. A form presumably derived from this species, described here as Sigmagraptus praecursor, differs only in the formation of two instead of four principal stems; and the development of the lower left and upper right principal stems of G. perflexilis into nondividing branches would directly lead to that type.

Fig. 42 Goniograptus perflexilis sp. nov. Enlargement of portion of branch of the specimen reproduced on plate 7, figure 7. Deep kill. x7

A peculiar feature of the largest specimen figured is a large, chitinous body, suggesting a collapsed bag, adhering to the initial part of the rhabdosome [pl.7, fig.9]. Whether this distinctly outlined structureless body is the remains of a central disk or of an unknown parasitic growth, it is impossible to decide by means of a single specimen. A central disk of the alate character observed in G. thureaui has not come to observation in this species.

The specimen obtained from the beds at Mt Moreno [pl.6, fig.16], if indeed belonging to this species, presents an extreme development of the flexible or flaccid character of the branches of the species. It has therefore been distinguished as *mutatio flaccida*. The apertures of its hairlike thecae are 2.5 mm apart and the thecae appear to be in contact not more than one fourth of their length.

### Goniograptus geometricus sp. nov.

Plate 7, figures 10-20

*Cf.* Thamnograptus anna Hall. Geol. Sur. Can. Canadian Organic Remains, decade 2. 1865. p.141, pl.21, fig.9

Goniograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.566

A surface of graptolite bed 3, belonging to the horizon with Didymograptus bifidus, is entirely covered with the rhabdosomes of an

extremely delicate multiramous dichograptid, but owing to their flexible nature the branches of the rhabdosome have, even by a very gentle current, nearly always been drifted into an inextricable mass; and, as at the same time innumerable specimens are piled together, it was found impos-

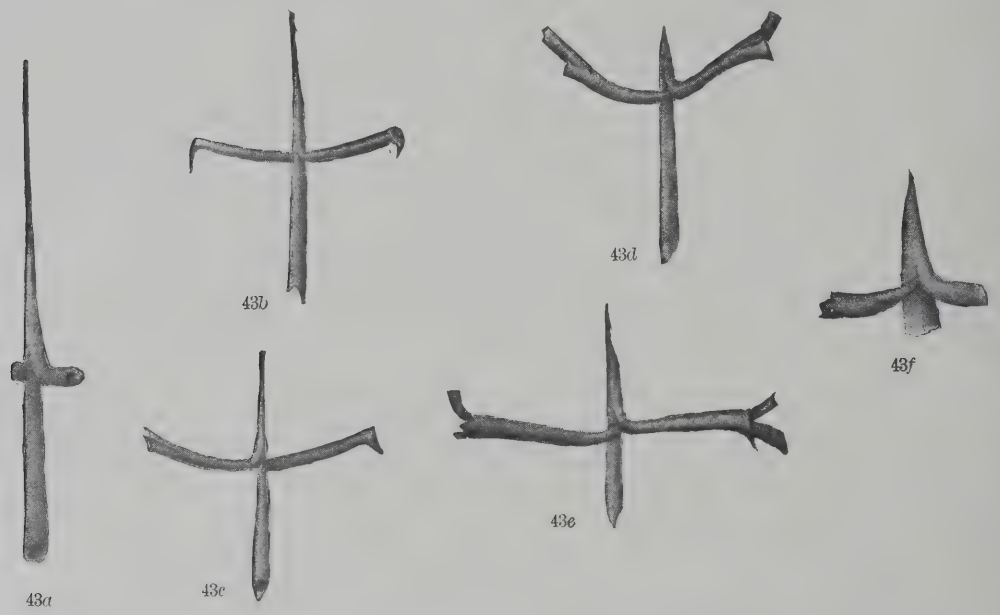


Fig. 43 Goniograptus geometricus sp. nov. *a* Sicula and proximal parts of first two thecae. Shows nema, which has become too thick in the zincograph. x8; *b* Growth stage with two thecae, which show apertural processes. x7; *c* Like growth stage, where the first theca originates nearer to the apex. x7; *d* Growth stage in which the first theca buds extremely close to the apex of the sicula and further dichotomy has set in. Reverse view. x7; *e* Young rhabdosome with relatively short or fragmentary sicula. Reverse view. x7; *f* Greater enlargement of first dichotomy. x21. Deep kill

sible to obtain specimens as well spread out as the type species of Goniograptus has furnished.

*Description.* Sicula long and narrow, needlelike, with an average length of 3.5 mm, but only a maximal width of .35 mm; in some instances provided with a long, very fine nema [fig.43a]. First theca budding within the apical fourth of the sicula; this and the second theca diverging at a point one fourth of the length of the sicula from the apical end in opposite directions and at right angles with the sicula. These first thecae are filiform (about 2 mm long), their free portions mostly straight, but often curved upward. The secondary thecae (forming the branches of the second

order), which equal the primary in length and width, diverge under angles of 120° to 150°; the four principal stems describe a zigzag line, the sections of which form an angle of 150°. The undivided denticulate branches stand at nearly right angles to the general direction of the principal stems. The thecae of the branches are tubular, narrow, about 2 mm long, three times as long as wide, one fourth to one third of their length in contact, numbering 8 in 10 mm, their outer margins nearly straight or slightly concave, the apertural margin straight and at right angles to the axis of the theca, inclined 10° to the axis of the branch. Total number of branches 40 or more; their length at maturity 30 mm or more. Central disk not observed.

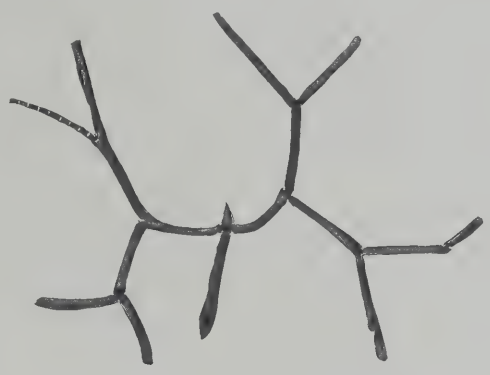

Fig. 44 Goniograptus geometricus sp. nov. Further enlargement of the specimen reproduced on plate 7, figure 12 to show the thecae forming the branches of the first, second and third orders. Deep kill. x5.25

*Position and localities.* Extremely common at the Deep kill in a layer of the horizon with Didymograptus bifidus, but already beginning in the preceding horizon.

*Remarks.* This species is closely related to the preceding one which occurs in the underlying horizon, differs, however, from it by the shorter length of the sicula and thecae, the very different angle of divergence and more compact arrangement of the branches. By the greater angularity of the zigzag shaped principal stems, it resembles more the type species of the genus than the foregoing species; but, like the latter, it differs from that species by the subapical budding point of the primary thecae at the sicula.

Fig. 45 Goniograptus geometricus sp. nov. Fragment of a branch. Deep kill. x5.25

I have little doubt that the specimen on which Hall based his species, Thamnograptus anna, was a branch of this or a very similar

species of Goniograptus, for it agrees in the zigzag form of the principal stem and the inclination of the branches fully with that delicate Goniograptus. The similarity is, in fact, so great that I did not hesitate at the preliminary identification of the Deep kill fauna to refer the numerous fragmentary branches of G. geometricus, occurring in that locality, to Thamnograptus anna [1902, p.566]. As, however, Hall expressly states that the branches of his species are filiform and do not show any thecae, while those of G. geometricus were found to bear distinct and prominent thecae, I did not feel justified to compare my material any longer with that species. It is however quite possible that in the type specimen of Thamnograptus anna the branches expose only their dorsal sides and for this reason do not show any thecae.

### LOGANOGRAPTUS Hall. 1867

The genus Loganograptus was erected by Hall and separated from the large generic group Dichograptus Salter for the reception of the single species Graptolithus logani Hall, and described [1867, p.226] by its author as being characterized by having its "polypary consisting of more than eight simple stipes proceeding from a single axis, with a distinct broad corneous disc." The genus is well defined and readily distinguished from the multiramous Clonograpti by its "simple stipes," resulting from the concentration of the dichotomy in the proximal region, and by the secondary disk. It is however connected by transitions so closely with Dichograptus *s. str.* as represented by Dichograptus octobrachiatus, that these two groups have been united by several authors (Herrmann, Frech) under Dichograptus.

But as each of these genera represents characteristic and important phylogenetic stages, which require recognition, they are retained here. Dichograptus *s. str.* marks that stage in the phylogenetic series leading from the multiramous forms to Tetragraptus, where the decline in the power of dichotomy has proceeded so far that branches of three orders only can be produced, the highest possible number of branches being then eight;

and Loganograptus denotes the preceding stage where the unlimited formation of branches in Clonograptus has become normally restricted to those of four orders only. Normally a Loganograptus has hence 16 branches; but imperfect fixation to branches of four orders on one hand, and incipient reduction to lower orders of branches on the other cause considerable variation in the number of branches. Thus in our material of L. logani there occur specimens with as many as 25 branches, there still being present branches of the fifth order, while, on the other hand, Elles and Wood mention specimens of the same species with but six branches where only one fourth dichotomy has taken place.

### Loganograptus logani Hall

Plate 9, figures 3-6

Graptolithus logani Hall. Geol. Sur. Can. Rep't. for 1857. 1858. p.115

Graptolithus logani Hall. Canadian Organic Remains, decade 2. 1865. p.100, pl.9, fig.1-9; pl.11, fig.7

Loganograptus logani Hall. N. Y. State Cab. Nat. Hist. 20th An. Rep't. 1867. p.226

Dichograptus logani Nicholson. Quar. Jour. Geol. Soc. 1868. 24:128

Loganograptus logani Nicholson. Monogr. Brit. Grapt. 1872. pt1, p.109, fig.52c, p.110

Graptolites (Didymograpsus) logani McCoy. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 1. 1874. p.19

?Loganograptus logani Etheridge jr. Ann. and Mag. Nat. Hist. ser. 4. 1874. 14:4, pl.3, fig.12

Non Loganograptus logani Etheridge jr. *Ibid.* pl.3, fig.11 (=Goniograptus thureaui)

Dichograptus logani Herrmann. Geol. Mag. Dec. 3, 1886. 3:24

*Cf.* Dichograptus kjerulfi Herrmann. Geol. Mag. ser. 3. 1886. 3:22, 23, fig.8

Loganograptus logani Ami. Geol. Sur. Can. Rep't. ser. 2. 1889. v.3, pt2, p.117k

Dichograptus logani Matthew. Roy. Soc. Can. Proc. and Trans. 1893. 11:114

Loganograptus logani Gurley. Jour. Geol. 1896. 4:294

Dichograptus logani Roemer & Frech. Lethaea palaeozoica. 1897. 1:595, fig.162

Loganograptus logani Elles. Quar. Jour. 1898. 54:476

Loganograptus logani Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556, 570

Loganograptus logani Elles & Wood. Monogr. Brit. Grapt. pt1. Pal. Soc. for 1902, p.81, pl.11, fig.1a-g

*Description.* Sicula, nema and primary disk not observed. Rhabdosome consisting of relatively long (about 2.1 mm) branches of the first order (funicle), dividing dichotomously into four short branches of the second order (about 1.4 mm long). Twice repeated dichotomous division in equally short intervals leads normally to 16 branches of the fourth order. Suppression of one or the other of the third dichotomies, or the appearance

Fig. 46 Loganograptus logani Hall. Enlargement of branch. Deep kill. x5.25

of fifth dichotomies on some of the branches results in variations in the number of the branches, commonly ranging in our material between 13 and 25. All dichotomy takes place within 5 mm from the sicula, or within the secondary disk. Branches of the last order very long (7½ inches and more according to Hall). Branches straight, narrow, of uniform width (.8 mm wide). Thecae numbering 8 to 10 in 10 mm, short, about three times as long as wide, in contact for about half their length, inclined at 30°, their outer margins very slightly concave, the apertural margins straight and inclined to the axis of the branch under an angle of 150°. Large secondary (central) disk present in larger specimens.

*Position and localities.* In graptolite bed 2 (Tetragraptus zone) occur fragments of branches which may belong to this species, but no proximal parts were noticed. In graptolite bed 7 (zone of Diplograptus dentatus) were found the specimens reproduced on plate 9, figures 3-6. Hall reports the species from the Point Levis beds; but

it can not be deduced from his work whether it occurs there in the lower or upper zone. Gurley, however, has observed it only among the graptolites of the upper Levis zone, hence at the horizon where it occurs in entire rhabdosomes at the Deep kill. Ami records it only from the island of Orleans, in an association insufficient for exact determination of the horizon. Matthew found it in division 3d of the St John group in New Brunswick. Nicholson, and Elles and Wood have described it from the Middle Skiddaw slates, which correspond to the two lower zones of the Deep kill; while in the latter place, as in Canada, it may be restricted to a higher zone, the Ellergill beds of north England. In Scandinavia it is represented by Dichograptus kjerulfi Herm., occurring in the lower Phyllograptus shales; and in Australia it has been recognized by McCoy among the graptolites of Castlemaine and other localities of the province of Victoria (described as a variety, characterized by wider branches and more robust thecae).

*Remarks.* The variability of the number of the branches of the last order in this species and its bearing on the phylogeny of the Dichograptidae have been discussed elsewhere. One of the stages, leading from L. logani to Dichograptus octobrachiatus, in which the number of branches had been at least locally fixed, is that represented by Dichograptus kjerulfi, which has not more than 12 branches.

In the Deep kill section the species rises a zone higher than in the other localities, from which it has been known. But these stragglers have the appearance of epacmic mutations of the species. One [pl.9, fig.5] is so reduced in all its dimensions, that I first thought it to be a new species, but now consider it more appropriate to distinguish it as a mutation, viz L. logani mut. pertenuis. This is characterized by extremely thin branches (in lateral view but .6 mm wide, in dorsal view .25 mm), very short thecae, numbering 10 to 12 in 10 mm, and inclined at the same angle as in the type of the species.

### DICHOGRAPTUS Salter. 1863 (modified)

The genus Dichograptus was erected by Salter [1863, p.139] and defined as follows: "Frond repeatedly dichotomous from a short basal stipe into 8, 16, 24 or more branches, each with a single row of cells." His Dichograpsus aranea, being the first form figured, would be the genotype, but, as it is a synonym of Hall's Graptolithus octobrachiatus, the latter becomes the type.

Later writers have successively separated groups of species under new generic terms from the assemblage of forms embraced by Salter's definition, and, following Lapworth's and Nicholson's example, restricted the genus Dichograptus to forms with eight branches of the third order, with D. octobrachiatus as genotype. Also, Hall used the term in this restricted sense [1863, p.226]. Elles [1898, p.483] and Elles and Wood define Dichograptus by the restriction of the formation of branches to that of three orders [*see* under Loganograptus, p.630], which gives eight branches as the maximal number.

As there are several species (D. octobrachiatus Hall, D. octonarius Hall and D. separatus Elles) known to have normally branches of three orders, this stage seems to be important enough to be designated by a separate name. For this reason we also use here the term Dichograptus, applying it in its restricted sense. The fact, however, that D. separatus belongs clearly to another evolutionary series than the other two species here cited [*see* Introduction, p.559], indicates that the group is of polyphyletic origin and not of generic value.

#### Dichograptus octobrachiatus Hall (sp.)

Plate 8, figures 1-7; plate 9, figures 1, 2

Graptolithus octobrachiatus Hall. Geol. Sur. Can. Rep't for 1857. 1858. p.122

Dichograpsus aranea Salter. Quar. Jour. Geol. Soc. 1863. 19:137, fig.9, 10

Graptolithus octobrachiatus Hall. Canadian Organic Remains, decade 2. 1865. p.96, pl.7, fig.1-7; pl.8, fig.1-4

Dichograpsus octobrachiatus Nicholson. Quar. Jour. Geol. Soc. 1868. 24:129, pl.5, fig.1, 2

Dichograptus octobrachiatus Nicholson. Monogr. Brit. Grapt. 1872. p.107, fig.50

Graptolites (Didymograpsus) octobrachiatus McCoy. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 1. 1874. p.17, pl.2, fig.4

Loganograptus kjerulfi Herrmann (*ex parte*) Nyt Mag. Naturv. 1882. 27:341-62

Dichograptus octobrachiatus Brögger. Die silurischen Etagen 2 and 3. 1882. p.38

Dichograptus octobrachiatus Herrmann. Nyt Mag. Naturv. 1885. 29:124

Dichograptus octobrachiatus Herrmann. Geol. Mag. Dec. 3, 1886. 3:22, fig.7

Dichograptus octobrachiatus Lecrenier. Ann. de la Soc. Géol. de Belg. 1887. 14:182

Dichograptus octobrachiatus et hexabrachiatus Malaise. Ann. de la Soc. Géol. de Belg. 1888. 15:40-44

Dichograptus octobrachiatus Ami. Geol. Sur. Can. Rep't, ser 2. 1889. v.3, pt2, p.117k

Dichograptus octobrachiatus Törnquist. Lunds Univ. Årsskrift. 1891. 26:12, pl.1, fig.1

Dichograptus octobrachiatus Gurley. Jour. Geol. 1896. 4:294

Dichograptus octobrachiatus Roemer & Frech. Lethaea palaeozoica. 1897. 1:595

Dichograptus octobrachiatus Elles. Quar. Jour. Geol. Soc. 1898. 54:483

Dichograptus octobrachiatus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p. 554,556

Dichograptus octobrachiatus Elles & Wood. Monogr. Brit. Grapt. pt1. Pal. Soc. for 1902. 1902. p.77, pl.9; pl.10, fig.1a-e

*Description.* Nema and primary disk not observed. Sicula apparently short and stout (about 1.1 mm long). Rhabdosome consisting of branches of three orders, those of the first order (funicle) together about 2 mm long, dividing dichotomously at either end. The four branches of the

second order measure 1.5 mm each. The latter produce normally by dichotomy eight branches of the third order, which, in the vertically compressed condition of the fossils, are straight, equidistant, very robust (maximum width of 3.6 mm observed), and attain a length of 10 cm (probably still much more, as indicated by separated branches). Thecae numbering 18 to 20 in 10 mm on large branches, and 20 to 22 in the same distance of more proximal portions, not quite four times as long as wide, in contact two thirds of their length, inclined at their bases at an angle of about 20°, but curving so that near the aperture the outer margin forms an angle of 50° to 55° with the axis of the branch; apertural margin straight or concave, forming an angle of 105° to 110° with the axis of the branch.

Adolescent and mature colonies possess mostly a secondary disk, extended between and slightly decurrent along the branches. It is roughly proportional in size to that of the rhabdosome and attained a diameter of 3 to 4 cm.

*Position and localities.* At the Deep kill common in the Tetragraptus horizon (very rare in graptolite bed 1, but very common in graptolite bed 2), rare in the zone with Didymograptus bifidus (graptolite bed 3). In the last zone (zone of Diplograptus dentatus, graptolite bed 7) only a single specimen of the hexad type [pl.8, fig.6] was observed. Hall's types came from the Point Levis shales, where, according to Gurley's observations, this species occurs only in the Main Point Levis zone (Tetragraptus zone). It is also found frequently in the Middle Skiddaw slates (Dichograptus beds) of north England and south Wales, the Phyllograptus shales of Christiania, Norway [Brögger & Herrmann], and of Dalarne, Sweden [Törnquist], and in Belgium [Lecrenier, Cluysenaar and Malaise]; and McCoy records it as common at various places in Victoria, Australia.

*Remarks.* This stately and regularly built graptolite was first described by Hall. Salter soon after termed two octobrachiate forms from

the Skiddaw slates Dichograpsus aranea and D. sedgewickii. We agree with Elles and Wood in considering the first of these names as a synonym of D. octobrachiatus, the differences being explicable by different modes of preservation.

Hall noticed already that the number of branches is not absolutely unvariable, but that suppression of a dichotomy may result in a smaller number of branches. Elles mentions a septad type, where one branch of the second order fails to divide dichotomously, and a hexad type, where two fail to divide. The only specimen of the hexad type noticed in our material was found in the uppermost Deep kill horizon (with Diplograptus dentatus), where the Dichograpti are rapidly disappearing.

Malaise observed a hexabrachiate form in Belgium and proposed for it the specific term D. hexabrachiatus [*loc. cit.* p.44]. This hexad variation occurs there also associated with octobrachiate forms, and in a high zone with Didymograptus murchisoni and Diplograptus pristiniformis (=dentatus), as in New York.

These occurrences show that there existed a tendency to reduction, which has finally led to the production of species of Tetragraptus [Introduction, p.567].

On the other hand we have observed, in graptolite bed 2, a form with nine branches in which one of the branches of the third order has divided again dichotomously, thus producing two branches of the fourth order [pl.8, fig.7]. While this form, by the strict application of the definitions of Loganograptus and Dichograptus, would have to be referred to the former stage, it is, in the character of the thecae and branches, and its general habit, a D. octobrachiatus. It is evident that hand in hand with the reduction of the number of branches other changes take place which make a strict application of this one criterion to the separation of the species impossible.

### BRYOGRAPTUS Lapworth. 1880

The genus Bryograptus was erected by Lapworth [1880, p.164] for forms with the following characters: "polypary bilaterally subsymmetrical, consisting of two compound monoprionidian branches diverging at a small angle from a well marked sicula, and originating similar compound (or single?) secondary branches at close but irregular intervals from one margin only. Hydrothecae minute, of the type of those of Dichograptus Salter."

This genus is remarkable for two facts, the irregularity of its branching and its early appearance. These facts and the great similarity of the species of Bryograptus to species of later genera with more regular branching indicate at once that the genus is a synthetic one, and stands in ancestral relation to various simple, more regularly branched graptolites. We have discussed these relations in the chapter on the classification and phylogeny of the graptolites [p.554], to which we refer the reader.

Elles and Wood have divided the British forms into two series, a dependent and a deflexed series. Each of these is represented at the Deep kill by one species.

The gemmation of the first thecae could be observed in B. lapworthi and has been described under that caption. It is like that of other Dichograptidae and specially like that of the Didymograptidae. The dichotomous branching also takes place in a manner identical with that described by the writer of Goniograptus thureaui and other Dichograptidae [1902, p.583], viz by the successive budding of two thecae, the second of which buds from the first, and both of which assume diverging directions.

The genus Bryograptus can be said to hover around the boundary line between Cambric and Siluric, for its species belong all either to the uppermost Cambric or lowest Lower Siluric, or to the transitional beds between the two, as B. kjerulfi, the genotype of this group, in the region of Christiania. In America thus far only some forms from the

St John basin, cited here under Staurograptus dichotomus [p.614], have been referred to that genus. In the Deep kill beds we have two new species termed B. pusillus and B. lapworthi.

It is a remarkable fact that the genus Bryograptus, which in Sweden and England is apparently restricted to the Upper Cambric beds[1] and which has also failed to be observed in the Canadian Levis beds, corresponding to the Deep kill horizon, persists here in the Tetragraptus beds with two species, one of which (B. pusillus) is extremely rare, while the other perfectly covers at least one layer and is also quite common as a component of the typical Tetragraptus fauna on other rock surfaces of the same bed.

### Bryograptus lapworthi sp. nov.

Plate 5, figures 1-12

Bryograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556

*Description.* The rhabdosome is suspended by a nema often relatively long, and very thin. This has in several cases been observed to be attached — in one case by means of a little chitinous node [fig.12] — to small chitinous blotches, supposedly the remains of a primary disk. The sicula is of medium size or rather short (1.2 mm in the average). The first theca originates close to the apex of the sicula, about one fourth of the length of the sicula from the same [fig.47]. This first theca produces the second one close to its own initial point and both these primary thecae diverge from the sicula each at an angle of about 110°, so that the average divergence between the proximal parts of the result-

Fig.47 Bryograptus lapworthi sp. nov. Young rhabdosome with fragment of primary disk. Obverse view. x6

[1] One exception, that of a species of B. ramosus var. cumbrensis on a slab with Tetragraptus bigsbyi, is noted by Miss Elles [1898, p.472].

ing branches is about 140° with variations, partly perhaps by somewhat oblique compression, to 100° on the one and to 170° on the other hand. The branches are in many specimens nearly straight in the initial part, in the majority, however, they have a slight concave curvature. The formation of the secondary branches [fig.7] is accomplished like that of the primary ones, by rapidly repeated gemmation [fig.11]. The secondary branches are disposed unsymmetrically, as the figures well illustrate, the bifurcation in the rhabdosome often taking place in one branch a short distance from the sicula, in the other very distally or not at all. In no case, however, has the bifurcation been observed so close to the sicula as in B. kjerulfi, callavei or ramosus. The branches are very slender, their maximum width being only about .5 mm.

The thecae are long, narrow tubes of nearly uniform width, or very slightly widening toward the aperture. They number quite constantly 10 in 10 mm, which number in a few cases sinks to 9, 8 or even 7; they are overlapping one third to one half of their length, are about five times as long as wide and diverge 15° to 20° from the axis of the branches. Their outer walls are straight or very slightly concave. The apertural margins are straight and form an oblique angle with the branch.

*Position and locality.* B. lapworthi is common in graptolite bed 1 and very common in graptolite bed 2 of the Deep kill section.

*Remarks.* This form is closely related to the specimen from the Lower Skiddaw slates at Barf, doubtfully referred by Marr [1894, p.130] and Elles [1898, p.470] to B. callavei Lapworth, and lately described by Elles and Wood as B. divergens. It, however, happens so that one difference between the specimen mentioned and the species described by Lapworth is here still more emphasized, i. e. the branches possess a still wider divergence. Moreover, the bifurcation of the branches in none of the specimens takes place so near to the sicula as in the specimen from Barf or in the types of B. callavei, though in this regard a great diversity prevails among the specimens, as is evinced by the figures [pl.5, fig.9, 10]. Our form differs from B. divergens, besides, in the

wider angle of divergence of the branches, in the somewhat closer arrangement and smaller angle of inclination of the thecae; in all other characters it agrees closely with that form. The British species occurs in a lower horizon than B. lapworthi.

### Bryograptus pusillus sp. nov.

Plate 4, figures 21, 22

Bryograptus kjerulfi (Lapworth) Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556

This species is represented by a single, well preserved specimen found on a slab from graptolite bed 2 (Tetragraptus bed).

*Description.* Rhabdosome small (6 mm long excluding the nema) consisting of a compact group of dependent branches. It begins with a long, delicate nema, to which a large relatively broad sicula (1 mm long) is attached. From this originate two primary branches at an angle of about 50°, each of which bifurcates into two secondary branches. The innermost of these divide again below the next theca. The earlier bifurcations take place symmetrically. The thecae which are disposed along the inner margins of the branches are long and narrow, four times as long as wide, slightly curved; they number 10 in 10 mm; overlap apparently not more than one fourth of their length, and form an angle of about 15° with the axis of the branch. The aperture is slightly concave; the apertural angle has not been accurately determined, but is larger than 90°.

*Position and localities.* A single specimen has been found on a slab of graptolite bed 2 with Tetragraptus caduceus.

*Remarks.* This form in its habit and specially in its mode of branching is a diminutive example of B. kjerulfi. I had, for this reason, originally referred it to that species, considering it a belated mutation of the same [1902, p.556]. The elaborate descriptions by Miss Elles and the exact drawings by Miss Wood, however, which have meanwhile appeared in the *Monograph of the British Graptolites*, allow a more conclusive comparison of our excellently preserved specimen with the European material of B. kjerulfi. By this we find that it differs from the latter

in having the thecae a little closer arranged, narrower and smaller and less overlapping, and all branches narrower and diverging more from each other at their bases. These differences, combined with the fact that B. kjerulfi occurs in Europe in a much deeper horizon (Bryograptus beds), make this form worthy of recognition as a separate species.

With this species the genus Bryograptus makes its last appearance in the graptolite beds of New York.

### TETRAGRAPTUS Salter

The genus Tetragraptus was proposed by Salter [1863, p.136] for forms in which "bifurcation takes place twice, the branches patent or

Fig.48 Tetragraptus similis Hall sp. Early growth stage of rhabdosome etched out of Vaginatenkalk of Oeland: *a* Obverse side showing sicula and first theca. *b* Reverse side showing the connecting canal. x12 (Copies from Holm)

nearly close." Thus defined, the "genus" embraces a wide range of forms, which, as noted before [p.554] belong to different phylogenetic series and have closer interrelations with species of other "genera" of like compass, as Didymograptus and Bryograptus, than with each other. The term, while eminently useful for a temporary grouping, is but an expression for a stage in the general progress of the class of graptolites and does not comprise a natural group of species of the same series. The genus as usually understood is hence polyphyletic; and should be subdivided into the natural groups quantivalent to a genus. The entirely different thecal character of a new form, [see T. lentus] which, under the present systematic arrangement, comes under Tetragraptus, emphasizes strikingly this demand of recent graptolithology. Such a grouping has been attempted by

Elles and Wood. These authors have divided the species according to the ultimate direction of their branches into series groups, some of which fall again into groups by the character of their thecae. In applying to our species of Tetragraptus this system, which, according to present knowledge, unites the members of phylogenetic series we obtain the following series and groups.

| | | | |
|---|---|---|---|
| Horizontal series | Group 1 | Type T. | quadribrachiatus |
| | | | T. quadribrachiatus |
| | | | T. amii |
| Dependent series | Group 2 | Type T. | fruticosus |
| | | | T. fruticosus |
| | | | T. clarkei |
| | Group 3 | Type T. | pendens |
| | | | T. pendens |
| Reclined series | Group 4 | Type T. | serra |
| | | | T. serra |
| | Group 5 | Type T. | similis |
| | | | T. similis |
| | | | T. woodi |
| | | | T. pygmaeus |
| | Group 6 | Type T. | taraxacum |
| | | | T. taraxacum |
| Flexuous (Etagraptus) series | Group 7 | Type T. | lentus |
| | | | T. lentus |

Holm has succeeded in isolating the rhabdosomes of a species of Tetragraptus (T. similis) and thus demonstrated that from the sicula near its apex originates a first theca, from which a second theca buds that turns to the other side. The development up to this stage is exactly homologous to that in Didymograptus. In each of the two diverging thecae a dividing wall appears, so that from each of these thecae two new thecae are originated. Each of the four resulting thecae becomes the mother theca of a branch. We have copied some of Holm's excellent drawings which illustrate this development [text fig.48-50].

Elles and Wood assert that in some forms, as in T. quadribrachiatus, the earliest thecae remain undivided, and the second or third theca on each side of the sicula undergoes division. The writer's material corroborates this statement, the correctness of which is already suggested by the greater relative length of the branches of the first order.

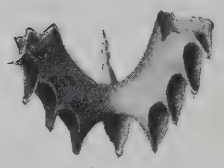

Fig.49 Tetragraptus similis Hall sp. Proximal part of a rhabdosome, seen from the left side. x6 (Copy from Holm)

We append here the description of a proposed subgenus which comprises group 7.

ETAGRAPTUS[1]

Plate 9, figures 7-10

The rhabdosome consists of two short central branches of the first order, from which on either side originate two branches of the second order, which, diverging in opposite directions and at right angles from the former, appear as two slender, flexuous undivided branches, corresponding to the vertical lines of an H, while the primary branches form the connecting bar. The sicula is long and the primary thecae diverge from the proximal part of the same.

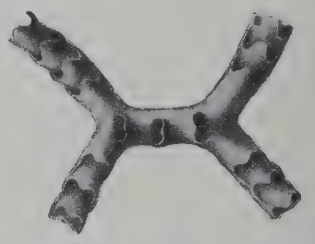

Fig.50 Tetragraptus similis Hall sp. Proximal part seen from below. Shows the apertures of the sicula (in the center), of the first two thecae and of those of the proximal portions of the branches. x6 (Copy from Holm)

This group has the same structure as Tetragraptus, viz a twice repeated bifurcation. It is, however, in the character of its thecae, the point of branching of the primary thecae and the direction assumed by the branches of the second order totally different from the other species of Tetragraptus; and it can be easily proved to belong to an entirely different series from the other four branched forms [ch.10, p.561]. The very slender thecae, the resulting very thin, flexuous branches, the peculiarly long sicula and, specially, the divergence of the primary thecae at a point high up near the apex indicate that T. (Etagraptus) lentus, the type of the subgenus belongs in one group with Goniograptus perflexilis, is closely

[1] In allusion to the similarity of its form to the Greek letter H.

related to Sigmagraptus praecursor and Coenograptus, though not their progenitor, and, very probably, leading to certain flexuous forms of Didymograptus.

### Tetragraptus quadribrachiatus Hall (sp.)

Plate 11, figure 1-4

Graptolithus quadribrachiatus Hall. Geol. Sur. Can. Rep't for 1857. 1858. p.125

Tetragrapsus crucialis Salter. Quar. Jour. Geol. Soc. 1863. 19:137, fig.8b

Graptolithus quadribrachiatus Hall. Canadian Organic Remains, decade 2. 1865. p.91, pl.5, fig.1-5; pl.6, fig.5,6

Tetragrapsus quadribrachiatus Nicholson. Quar. Jour. Geol. Soc. 1868. 24:131

*Cf.* Graptolites (Didymograpsus) quadribrachiatus McCoy. Jour. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 1. 1874. p.15, pl.2, fig.1

Non Tetragraptus quadribrachiatus Etheridge jr. Ann. and Mag. Nat. Hist. ser. 4. 1874. 14:3, pl.3, fig.5-8

Tetragrapsus quadribrachiatus Hopkinson & Lapworth. Quar. Jour. Geol. Soc. 1875. 31:649, pl.33, fig.9a, 9b

Tetragraptus quadribrachiatus Linnarsson. Sver. Geol. Und. 1879. Afh. och upps. ser. C, no.31, p.5

Tetragraptus quadribrachiatus Brögger. Die sil. Etagen 2 and 3. 1882. p.38

Tetragraptus quadribrachiatus Törnquist. Sver. Geol. Und. 1883. Afh. och upps. ser. C, no.57, p.16

Tetragraptus quadribrachiatus Herrmann. Quar. Jour. Geol. Soc. 1886. ser. 3, 3:18

Tetragraptus quadribrachiatus Barrois. Ann. de la Soc. Géol. du Nord. 1892. 20:95

Tetragraptus quadribrachiatus Matthew. Roy. Soc. Can. Trans. and Proc. 1893. 11:114

Tetragraptus quadribrachiatus Gurley. Jour. Geol. 1896. 4:295

Tetragraptus quadribrachiatus Roemer & Frech. Lethaea palaeozoica. 1897. 1:603

Tetragraptus quadribrachiatus Elles. Quar. Jour. Geol. Soc. 1898. 54:485

Tetragraptus quadribrachiatus Ruedemann. N. Y. State Paleontol. An Rep't. 1902. p.556

Tetragraptus quadribrachiatus Elles & Wood. Monogr. Brit. Grapt. pt1. 1902. p.57, pl.5, fig.1a-d

*Description.* Primary disk and nema not observed. Sicula present, but observed only in sections. Branch of first order 2.6 mm long, consisting apparently of two thecae on either side. Four branches of the second order, which are spread out horizontally; straight, slender, rigid, increasing very gradually from a width of .6 mm to one of 2.4 mm, attaining a maximal length of 42 mm. Thecae 8 to 9 in 10 mm, inclined at a low angle (about 35-40°), narrow (four times as long as wide), overlapping for one half to one third of their length. Outer wall slightly curved. Apertural margins straight or slightly concave, normal on the axis of the thecae.

Fig. 51 Tetragraptus quadribrachiatus Hall sp. Young rhabdosome. Deep kill. x4.5

*Position and localities.* In the Deep kill section this species has been found in great number in graptolite bed 2 (Tetragraptus zone), less common in bed 5 and in but a single specimen in graptolite bed 7 (zone with Diplograptus dentatus)[1]. It is also common in a band of sandy slate, outcropping between Defreestville and West Sandlake, Rensselaer co. N. Y. [T. N. Dale, coll.]; and one small specimen has been observed in the shales with Diplograptus dentatus at Mt Moreno near Hudson N. Y.

Hall's specimens came from the lower shales of Point Levis (Tetragraptus horizon or Main Point Levis zone of Gurley). Matthew collected it also in the St John basin. In Great Britain the species occurs in the middle and upper beds of the Middle Skiddaw slates in the Lake district at numerous localities; in the St David's district in Wales and in the Ballantrae

[1]The latter may belong to a somewhat different later mutation, as the greater proximal width of its branches would suggest, but it is not in a sufficiently good state of preservation to decide this point.

district in south Scotland. Brögger records it from the region of Christiania, the Swedish authors from Dalecarlia and the Tetragraptus zone in Scania. Barrois cites it as being rare in the graptolite schists at Cabrières in the Languedoc, and McCoy reports it from the shales of Victoria, Australia.

*Remarks.* Hall said of this species, that it, "when entire, is readily distinguished from Graptolithus bryonoides by its straight and more slender branches, and by the general aspect and expression of the fossil." Indeed, the geometric regularity of the disposition of the branches in the compressed material, combined with their slenderness, will readily serve as a distinctive character, even where the various species of Tetragraptus are promiscuously mixed, as in graptolite bed 2. On account of the original horizontal position of the branches and the downward direction of the thecae, with rare exceptions only the dorsal or ventral side is exhibited, and the profile view can be observed only when, as in the original of figure 3, the branches were, during entombment, turned to one side. Also on account of this position of the rhabdosome the sicula is, in the shale, always embedded in its natural vertical position and therefore only seen in sections.

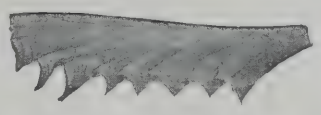

Fig. 52 Tetragraptus quadribrachiatus Hall sp. Portion of branch enlarged. Deep kill. x3.2

The horizontal and rigid position of the branches is evidently largely due to the character of the dorsal perisarcal wall of the coenosarcal canal, which in the flattened specimens alone projects bodily and appears like a solid axis. The same feature is found still more emphasized in T. amii, evidently on account of its broader and correspondingly heavier branches.

### Tetragraptus amii Lapworth ms. (Elles & Wood em.)

Plate 11, figures 5-7

Graptolithus bryonoides Hall (pars). Geol. Sur. Can. Grapt. Quebec Group. Figures and Descriptions, decade 1. 1865. p.84, pl.4, fig.9, 10

Tetragraptus amii Elles & Wood. Monogr. Brit. Grapt. 1902. pt1. Pal. Soc. p.60, pl.5, fig.4a-c

*Description.* Primary disk and nema not observed. Sicula inconspicuous, about 2 mm long. Branches of first order (consisting of one theca) narrow (.5 mm), 3.1 mm long. Four branches of second order or main stipes disposed horizontally, having a normal length of 30 cm, but attaining a maximal length of 60 mm and more; those of either side forming angles ranging between 70° and 90°, widening within a few millimeters from the point of bifurcation to the maximal width (2.9 to 3 mm), which is maintained to near the distal end. Thecae slightly curved, numbering 9 to 10 in 10 mm, about 3 mm long, inclined at 40° in their average, of uniform width, three to four times as long as wide, and overlapping about three fourths of their length. Outer walls concave, apertural margin concave, normal to the axis of the theca.

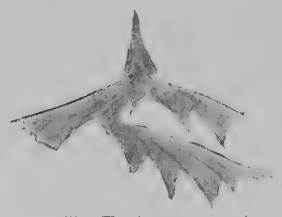

Fig. 53 Tetragraptus amii L., E. & W. Young rhabdosome; one branch missing. Reverse view. Shows point of origin of first theca and direction of proximal portions of branches. Deep kill. x4.

*Position and localities.* Hall does not state the locality of the specimen which is referred by Elles and Wood to their new species. At the Deep kill we have observed this form only in graptolite bed 2 (Tetragraptus zone), where it is found associated with T. serra, T. fruticosus, Phyllograptus ilicifolius, Didymograptus extensus, etc. The authors of the species record it from the Middle Skiddaw slates, in association with some of the species just mentioned; and from south Wales.

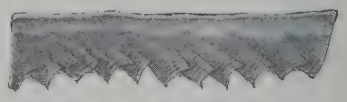

Fig. 54 Tetragraptus amii L., E. & W. Fragment of branch. Deep kill. x3.3

*Remarks.* Elles and Wood state in their work that this form was included by Hall (with doubt) in T. bryonoides (=serra), and that Lapworth long considered it as distinct. Also, the present writer had recognized the differences between this form and T. serra, when the description of the species was published. While the dimensions and characters of the branches and thecae are the same as in T. serra, the branches are here disposed horizontally, instead of being reclined as in that form. This difference is most strikingly

shown in the numerous young specimens, which frequently become compressed laterally. In this mode of preservation, in T. serra the four branches diverge fully [pl.11, fig.8]; while in T. amii they coincide more or less [pl.11, fig.7].

From T. quadribrachiatus, which possesses the same horizontal disposition of the branches, this species is readily distinguished by the rapid widening of the branches.

A feature still more distinctly developed in this species than in the other congeners is the thickness of the dorsal wall of the coenosarcal canal [p.552, pl.11, fig.5].

### **Tetragraptus fruticosus** Hall sp.

Plate 9, figures 11-14; plate 10, figures 1-10

Graptolithus fruticosus Hall. Geol. Sur. Can. Rep't for 1857. 1857. p.128

Graptolithus fruticosus Billings. Geol. Sur. Can. Pal. Foss. 1865. 1:366,375

Graptolithus fruticosus Hall. Canadian Organic Remains, decade 2. 1865. p.90, pl.5, fig.6-8

Graptolithus fruticosus Hall. N. Y. State Cab. Nat. Hist. 20th An. Rep't. 1867. pl.3, fig.15

Didymograptus? fruticosus Etheridge jr. Ann. and Mag. Nat. Hist. ser. 4. 1874. 14:6, pl.3, fig.19

Graptolites (Didymograpsus) fruticosus McCoy. Jour. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 1. 1874. p.13, pl.1, fig.9-14

Tetragraptus fruticosus Lapworth. Ann. and Mag. Nat. Hist. ser. 5. 1880. 6:20

Tetragraptus (Bryograptus?) fruticosus Brögger. Die sil. Etagen 2 and 3, etc. 1882. p.39

Tetragraptus fruticosus Tullberg. Sver. Geol. Und. 1882. Afh. och upps. ser. C, no.50, p.22

Tetragraptus fruticosus Lapworth. Roy. Soc. Can. Proc. and Trans. 1886. p.168

Tetragrapsus fruticosus Ami. Geol. Sur. Can. Rep't. ser. 2. 1889. v.3, pt2, p.116k

Tetragrapsus fruticosus Gurley. Jour. Geol. 1896. 4:295

Tetragraptus fruticosus Roemer & Frech. Lethaea palaeozoica. 1897. Bd1, p.602

Tetragraptus fruticosus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.554, 556, 566; p.588, fig.15

Tetragraptus fruticosus Elles & Wood. Monogr. Brit. Grapt. pt1. Pal. Soc. vol. for 1902. 1902. p.61, pl.6, fig.2a, b

*Description.* Sicula long (about 3.6 mm), and slender. Provided in young colonies with a short, thin nema which in one case [pl.9, fig.14] has been observed to terminate in a small concentrically wrinkled, chitinous disk (diameter = 1.3 mm). Mature rhabdosome suspended by means of a long, stout nema, or nemacaulus, which attains a width of 1.5 mm (in compressed state) and gradually tapers to a fine thread. Total length of nema unknown, but in a mature specimen a fragment of 30 mm in length has been observed, which did not show any decrease in its width. First theca budding in the apical third of the sicula; first and second thecae adhering to the sicula till near its aperture; each of these thecae producing two branches by dichotomy. Two pairs of gracefully and symmetrically curved branches, which give to the rhabdosome a bell or lyre-shaped outline; the branches attain a length of 10 cm and more, and a width of 3.5 mm, and diverge at an angle of about 40°. The reflection of the branches takes place at various distances (18 to 48 mm) from the aperture of the sicula. The branches increase gradually in width up to the point of reflection, when they become approximately uniform in width. Thecae short and broad in the proximal parts of the branches, long, narrow and mucronate in the mature parts, six being counted in the space of 10 mm in the former and eight within the same space in the latter. The early thecae overlap about one half their length, the mature ones are in contact nearly their entire length; the former form an angle of about 20° with the axis of the stipe, the latter one of 40°; the apertural margins of the nepionic thecae are straight, their upper margin is not protracted into a mucro, while the apertural margins of the mature thecae are deeply concave and their upper margins mucronate.

*Position and localities.* T. fruticosus has, at the Deep kill, been collected in graptolite beds 1 and 2. In both beds which belong to the Tetragraptus zone, it occurs in much larger specimens than have been hitherto recorded; and with the forms found in bed 2 it reached distinctly the acme of its development. In bed 3 (zone with Didymograptus bifidus and Phyllograptus anna) it is not found any longer at the Deep kill in its typical development. Hall reported the form from "the shales of the Quebec group at the upper end of Orleans island, and three miles above river St Anne." Ami records it from three localities near Levis, in two of which it is a member of the Didymograptus bifidus fauna, while in the third it is one of the Tetragraptus fauna. Gurley lists it as occurring in the "Main Point Levis zone" and the "Phyllograptus anna zone," which range tallies with that at the Deep kill and with Ami's results. Billings identified graptolites from the division P at Cowhead, Newfoundland, with this Quebec species. In Britain it is, according to Elles's reports and those of the monographers, poorly represented, but occurs in the Arenig of south Scotland and of the Lake district. In Sweden and Norway it is found in the Phyllograptus shale (*fide* Törnquist, Tullberg and Brögger); in Australia, McCoy has declared specimens from various outcrops of the Lower Siluric slate in Victoria to be "perfectly identical in all respects with the North American species."

*Remarks.* From the figures or descriptions furnished by the authors, cited above, it can be concluded that they had either only immature specimens or proximal parts, or small mutations before them. As our series contains excellent, fully developed specimens and exhibits division into two variations, we have been able to enlarge the original description considerably. The difference in the character of the earlier and later thecae of the branches has been pointed out before by the writer [1902, p.589], and its phylogenetic significance set forth [*see also* Introduction, p.531].

In the Tetragraptus bed there occur two greatly differing variations of the form, which however are sufficiently connected by transitional forms to warrant their retention within the bounds of one species. In one, the

more common form, the reflection of the branches takes place at quite a distance from the sicula, or initial part of the rhabdosome, and the proximal portion of the branches possesses a convex outer margin. The outline of these rhabdosomes is such as to suggest a section of a bell. We will therefore designate this variety, which is the one originally observed by Hall, as T. fruticosus campanulatus [pl.10, fig.7].

Very different in habit from this are forms which the writer at first believed to represent a different species [pl.10, fig.2]. The proximal parts of their branches diverge stronger, are concave toward the outside, and the reflection takes place considerably earlier. The result is an outline suggestive of a trumpet; and we designate this variety as T. fruticosus tubiformis. This variety approaches Didymograptus V-fractus Salter so much that it suggests itself as the progenitor of that species.

The nema or nemacaulus of this species is in large specimens inflated in the middle and may have been filled with gas to aid in supporting the stout rhabdosome.

### **Tetragraptus clarkei** sp. nov.

Plate 11, figures 11-16

Tetragraptus fruticosus mut. (*pars*). Ruedemann. N. Y. State Paleontol. An. Rep't 1902. p.566

*Description.* Primary disk and nema not observed. Sicula long (2.6 mm), conspicuous, slender. Four branches dependent, strongly divergent approximately under right angles, curved outward, widening rapidly from a width of .5 mm at their basis to one of 2.6 mm or more. Thecae, in the mature portion of the branches numbering 9 to 10 in 10 mm, relatively broad, two to three times as long as wide, about 3 mm long, inclined at an angle of 30°, overlapping for one half to two thirds of their length; straight, their outer walls and apertural margins straight, the latter normal on the axes of the thecae.

*Position and localities.* T. clarkei has been found only in graptolite bed 3, associated with Goniograptus geometricus, Goniograptus thureaui, Didymograptus similis and Didymograptus bifidus.

*Remarks.* This species, which originally was considered a later mutation of T. fruticosus, has evidently been derived from that species, but by the process of acceleration, the geniculation and the widening of the branches take place so closely to their bases and so rapidly, that this form bears a greatly different aspect from the typical T. fruticosus. As it also differs in the arrangement of the thecae and is restricted to another horizon, it has the morphologic and stratigraphic value of a separate species. The thecae are more closely arranged than in the mature branch of T. fruticosus, but at the same time they do not develop some of the mature features of those of T. fruticosus, as they do not become so strongly inclined, do not overlap so much and do not possess the conspicuous apertural mucros of the progenitor. In general outline they are clearly a fuller development of the variety which I have designated as T. fruticosus tubiformis. The earliest thecae of the branches agree still with those of the like stage in T. fruticosus.

The characters of the proximal parts of the rhabdosome, specially the origin of the first thecae, have not been seen with sufficient distinctness to warrant their description.

### **Tetragraptus pendens** Elles

Plate 11, figures 17-20

Tetragraptus pendens Elles. Quar. Jour. Geol. Soc. Lond. 1898. 54:491, fig.13

Tetragraptus pendens Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.566

Tetragraptus pendens Elles & Wood. Monogr. Brit. Grapt. Pal. Soc. for 1902. p.61, pl.6, fig. 2a, b

On slabs derived from the Didymograptus bifidus zone occur frequently specimens of a small Tetragraptus which have been identified with a form described by Miss Elles from the Middle Skiddaw slates. From the species cited as being associated with it (Phyllograptus cf. typus, Didymograptus gibberulus) in the English Lake region, we infer that this organism occurs here in beds homotaxial to the English.

While in general form, size and aspect the form closely agrees with the figures given of T. pendens, there appear some small differences in the measurements which are thought to be too insignificant to indicate a variety.

The rhabdosome is small (14 mm greatest length observed), slender (5.5 mm greatest width observed), consisting of four dependent branches which are subparallel or approach slightly distally, forming long, flat crescents. The sicula is relatively short (1.3 mm) and rapidly widening. The thecae open toward the inner side of the rhabdosome, increase only slightly in width, and the branches are therefore of nearly uniform width. The thecae are long, slender tubes (length 1.6–2 mm), which at the beginning of the branches do not overlap more than $\frac{1}{4}$ of their length, the overlap increasing to not quite $\frac{1}{2}$ of their length. Eight to 10 thecae were counted within the space of 10 mm. The angle of inclination of the thecae increases to 20° or even 22° when the branch assumes mature features. The outer margins of the thecae are slightly concave, with a small increase of the curvature near the aperture. The apertures are straight or slightly concave, and they form an angle of about 110° with the axis of the branches.

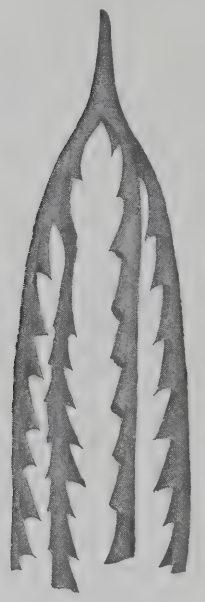

Fig. 55 Tetragraptus pendens Elles. Enlargement of proximal portion of rhabdosome to show the character of sicula and thecae. Deep kill. x4.5

*Position and localities.* In the zone with Didymograptus bifidus and Phyllograptus anna, on slabs with Didymograptus bifidus and Goniograptus geometricus. In Great Britain it occurs in the Middle Skiddaw slates of the Lake district, associated with Didymograptus (gibberulus) caduceus and Phyllograptus cf. typus.

*Remarks.* It has been pointed out by the author of the species that it is related to T. fruticosus, but readily distinguished from the latter more common type by its much more slender form, the more uniform width of the branches, closer arrangement of the thecae and smaller angle of inclina-

tion. In regard to the latter feature this species approaches the nepionic part of the branches and thus appears as a more primitive form. It could therefore be taken for a derivative of T. fruticosus in a state of arrested development, and lacking the tendency to reclination. The dependent position of the branches in this species is also maintained in its closest genetic relative, Didymograptus (indentus) dentatus.

### Tetragraptus serra Brongniart sp.

Plate 11, figures 8-10

Fucoides serra Brongniart. Hist. Végét. Foss. 1828. 1:71, pl.6, fig.7, 8
Didymograpsus caduceus Salter (*pars*). Quar. Jour. Geol. Soc. 1853. 9:87, fig.1a
Graptolithus bryonoides Hall. Geol. Sur. Can. Rep't for 1857. 1858. p.126
Tetragrapsus (bryonoides) Salter. Quar. Jour. Geol. Soc. 1863. 19:137, fig.8
Didymograpsus caduceus Salter. *Ibid.* p.136
Graptolithus bryonoides Hall (*pars*). Canadian Organic Remains, decade 2. 1865. p.84, pl.4, fig.1–8, 11
Graptolithus bryonoides Billings. Geol. Sur. Can. Pal. Foss. 1865. 1:366, 375
Tetragrapsus bryonoides Nicholson. Quar. Jour. Geol. Soc. 1868. 24:131
Graptolites (Didymograpsus) bryonoides McCoy. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 1. 1874. p.15, pl 2, fig.2, 3, 5
Tetragraptus quadribrachiatus Etheridge jr. Ann. and Mag. Nat. Hist. ser.4. 1874. 14:3, pl.3, fig.5–8
Tetragraptus bryonoides Etheridge jr. (*pars*) *Ibid.* p 2, pl.3, fig.1
Tetragraptus serra Hopkinson & Lapworth. *Ibid.* 1875. 31:650, pl.33, fig.10
Tetragraptus bryonoides Linnarsson. Sver. Geol. Und. 1879. Afh. och upps. ser.C, no.31, p.5
Tetragraptus bryonoides Brögger. Die sil. Etagen 2 and 3. 1882. p 38
Tetragraptus bryonoides Tullberg. Skånes Grapt. in Sver. Geol. Und. 1882. Afh. och upps. ser.C, no.50, p.22
Tetragraptus serra Törnquist. Sver. Geol. Und. 1883. Afh. och upps. ser.C, no.57, p.16
Tetragraptus serra Herrmann. Geol. Mag. ser.3. 1886. 3:19
Tetragraptus serra Ami. Geol. Sur. Can. Rep't, ser.2. 1889. v.3, pt2, p.116k

Tetragraptus serra Barrois. Ann. de la Soc. Géol. du Nord. 1892. 20:94
Tetragraptus serra Gurley. Jour. Geol. 1896. 4:295
Tetragraptus bryonoides Römer & Frech. Lethaea palaeozoica. 1897. 1:601
Tetragraptus serra Elles. Quar. Jour. Geol. Soc. 1898. 54:490
Tetragraptus serra Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.554, 556, 566
Tetragraptus serra Elles, Wood & Lapworth. Monogr. Brit. Grapt. pt1. Pal. Soc. 1902. p.65, pl.6, fig.4a-f

*Description.* Primary disk and nema not observed. Sicula relatively short (2 mm) and slender. First theca originating within apical third of sicula. Branch of first order (first two thecae) short, about 2.7 mm long; four branches of the second order approximately straight, attaining a length of 30 to 50 mm, rapidly widening from .7 mm to the threefold and fourfold width. Thecae 8 to 9 in 10 mm, narrow (three to four times as long as wide), slightly curved, much inclined (40° to 45°), overlapping for two thirds to three fourths of their length. Outer thecal walls concave, apertural margin concave, normal on axis of thecae.

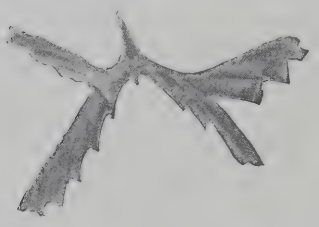

Fig. 56 Tetragraptus serra Brongniart *sp.* Young rhabdosome. Obverse view. Deep kill. x4.5

*Position and localities.* Brongniart's original of the species came from Point Levis; and Hall based his description on material from Quebec shales of Point Levis, Gros Maule and River St Anne. The form is evidently very common in the Levis region; for Ami cites it from a whole series of localities in that neighborhood. Gurley lists T. serra as occurring in all three Quebec zones, the Main Point Levis zone, the Phyllograptus anna zone and the Upper Levis zone. Besides, he found it also in the suite submitted to him from Arkansas. Billings noted the species among the graptolites from Cowhead, Newfoundland (division P).

In the preliminary paper on the Deep kill section, I reported this form as being rare in graptolite bed 1, common in graptolite bed 2, as being found in a small mutation in graptolite bed 3, and as passing through the Didymograptus bifidus zone (graptolite beds 3 to 5). It occurs also associated with Dictyonema murrayi, a species of Clonograptus and

T. quadribrachiatus in a sandy slate between Defreestville and West Sandlake, Rensselaer co. N. Y. [T. N. Dale, coll.] In the second instalment of the *Monograph of the British Graptolites*, which has just appeared, the species as defined by Hall has been split and a part separated as T. amii. This new species is common in graptolite bed 2, and its separation will make T. serra a less frequent form in that bed. Also the form, listed as a smaller mutation of T. serra from the zone of Didymograptus bifidus, must be separated as a new species. T. serra, thus limited, is in the Deep kill section restricted to the first two beds (zone with Tetragraptus.)

In Great Britain the form has long been known by Salter's, Nicholson's, Lapworth's and Hopkinson's investigations. It occurs there in the upper beds of the Middle Skiddaw slates, associated with like forms as in America; in the Lake district, in south Scotland and in south Wales.

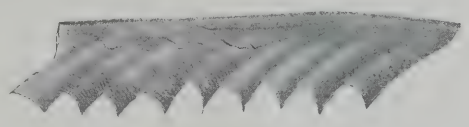

Fig. 57 Tetragraptus serra Brongniart *sp.* Fragment of branch. Shows the form and inclination of the thecae; and the thick dorsal wall of the coenosarcal canal. Deep kill. x4.8

In Scandinavia it is known to occur in Tetragraptus shales in the region of Christiana [Brögger], in Skåne [Tullberg], West Gothland and Dalecarlia. Barrois records it among the fossils from the graptolite schists of Boutoury near Cabrières in southern France, and it was early found in Victoria, Australia.

*Remarks.* This species exhibits also the strengthening of the branches by a thickening of the dorsal wall of the coenosarcal canal, mentioned in the descriptions of T. quadribrachiatus and T. amii. As it agrees in nearly all essential features, except the direction of the branches, with the latter, there is little doubt that it is derived from that species and marks a further stage in the process of the gradual elevation of the originally dependent branches into a reclined position by way of a horizontal disposition.

The young of this species, which are quite common in graptolite bed 2, possess a characteristic aspect, by having been compressed in such a fashion that two branches appear to have a dependent and two a reclined position [pl.11, fig.8].

## Tetragraptus similis Hall (sp.)

Plate 12, figures 2–10

Phyllograptus similis Hall. Geol. Sur. Can. Rep't for 1857. 1858. p.140
Didymograpsus caduceus Salter? Quar. Jour. Geol. Soc. 1863. 19:137, fig.13b(?)
Graptolithus bigsbyi Hall. Canadian Organic Remains, decade 2. 1865. p.86, pl.16, fig.22–30
Didymograptus caduceus Nicholson. Quar. Jour. Geol. Soc. 1868. 24:133
Tetragraptus bryonoides Etheridge jr. Ann. and Mag. Nat. Hist. ser.4. 1874. 14:2, pl.3, fig.1, 2; non fig.3, 4
Tetragraptus bigsbyi Linnarsson. Sver. Geol. Und. 1879. Afh. och upps. ser.C, no.31, p.5
Tetragraptus bigsbyi Tullberg. *Ibid.* 1882 ser.C, no.50, p.22
Tetragraptus caduceus Brögger. Die sil. Etagen 2 and 3. 1882. p.38
Tetragraptus bigsbyi Ami. Geol. Sur. Can. Rep't, ser.2. 1889. v.3, pt2, p.116k
Tetragraptus caduceus Perner. Études sur les Grapt. de Bohême, pt2. 1894. p.20, pl.6, fig.9–12
Tetragraptus bigsbyi Holm. Sver. Geol. Und. 1895. Afh. och upps. ser.C, no.150, p.24, pl.1, fig.9–16; pl.2, fig.1–3; pl.3, fig.13–16
Tetragraptus bigsbyi Holm. Geol. Mag. Dec. 4, 1895. 2:484, pl.13, fig.9–16; pl.14, fig.13–16; p.485, fig.1–3
Tetragraptus bigsbyi Gurley. Jour. Geol. 1896. 4:294
Tetragraptus bigsbyi Roemer & Frech. Lethaea palaeozoica. 1897. 1:600, 601, fig.166
Tetragraptus bigsbyi Elles. Quar. Jour. Geol. Soc. 1898. 54:488
Tetragraptus bigsbyi Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556, 566
Tetragraptus bigsbyi Elles & Wood. Monogr. Brit. Grapt. pt1. Pal. Soc. for 1902. 1902. p.68, pl.6, fig.6a-e
Non Didymograpsus caduceus Salter. Quar. Jour. Geol. Soc. 1853. 9:87, fig.1a
Non Graptolites (Didymograpsus) caduceus McCoy. Prodr. Pal. Victoria, decade 1. 1875. p.16, pl.2, fig.2, 3, 5
Non Tetragraptus bigsbyi Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.590, fig.18

*Description.* Small subcircular primary disk and very thin filiform nema. Rhabdosome of small size (usual length about 12 mm); forming a broad oval in younger, a more elongate truncate oval in older specimens; consisting of four relatively wide branches (1.6 mm at their origin, rapidly attaining a width of 2.5 mm and diminishing again toward the extremity), which in most specimens are straight or slightly concavely curved on the dorsal side and present a stronger convex outline on the frontal side.

Sicula about 2.1 mm long, stout. Branches of the first order monothecal, each 1.1 mm long. Those of the second order short (rarely exceeding 13 mm in length), in typical specimens flexed, curving upward and inward. Thecae

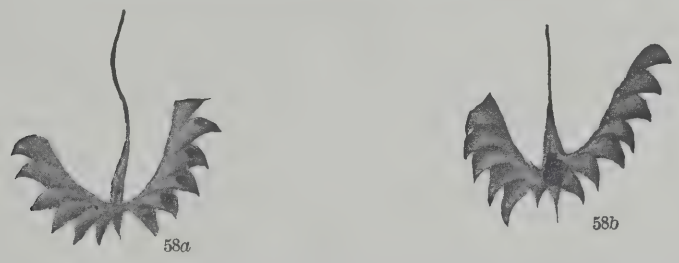


Fig. 58 Tetragraptus similis Hall *sp.* Two specimens, in which only the branches of one side are retained; in *a* the branches are seen from the outside; in *b* from the inside of the rhabdosome. Deep kill. x5.25

numbering 10 to 14 in the space of 10 mm, gradually ascending (initial angle about 50°), but curving outward in their distal parts (angle 60° to 70°), widening toward the aperture, four times as long as wide; in contact four fifths of their length. Apertural and external margins slightly concave, both forming a characteristic recurving, mucronate apertural denticle.

*Position and localities.* Occurring in great profusion in the Tetragraptus bed of the Deep kill, specially graptolite bed 2, still met in scarce and depauperated specimens in graptolite bed 3, which represents the lower part of the zone with Didymograptus bifidus.

This species, which in mature representatives, is very readily recognized by the curved, relatively broad branches and the curved apertural denticles, is evidently a form of vast distribution. It was originally described by Hall as occurring in great multitudes in the Quebec shales at Point Levis, where

according to Gurley it is found in the Main Point Levis or Tetragraptus zone. Ami cites it also from two localities near Levis together with Didymograptus bifidus. In Britain it is known from many localities in northern England and south Scotland, where it occurs in the Lower and Middle Skiddaw slates. It is further recorded by Brögger from the lower part of the Phyllograptus shale at Krekling, Christiania, Norway; from the Tetragraptus zone of Scania by Tullberg; and the gray Orthoceras limestone of Oeland furnished to Holm the material of this species, on which he based his investigation of the structure of Tetragraptus; Perner describes T. bigsbyi from band Dd1$^{\beta}$ of the Bohemian Lower Siluric, the occurrence of this species in Bohemia having before been reported by Törnquist; in Australia, finally, it has been recognized by the younger Etheridge in the auriferous graptolite shale of Victoria.

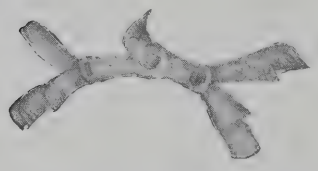

Fig. 59 Tetragraptus similis Hall *sp.* Young compressed rhabdosome seen from the under side. Shows the apertures of the sicula and first two thecae. Deep kill. x6

*Remarks.* Specimens in which the distal ends of the branches had been in contact, either by compression or natural position, had been described by Hall as Phyllograptus similis, a name which was withdrawn later on by its author on account of the supposed precedence of his species Graptolithus similis. Since the latter belongs to another genus (Didymograptus), the term T. similis would, according to the present rules of priority, have to stand against the later and generally adopted name, T. bigsbyi.

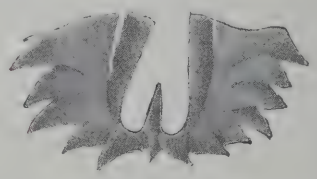

Fig. 60 Tetragraptus similis Hall *sp.* Proximal portion of rhabdosome. Obverse view. Deep kill. x4.5

Our list of synonyms demonstrates that several authors have referred this species to Salter's Didymograptus caduceus. We shall show under that heading [p.696] that Salter figured under this name a specimen of Didymograptus and a fragment of T. similis Hall; and that according to the rules of priority his name will have to be applied to the first figured form, i. e. to Didymograptus caduceus. In no case can Salter's name be employed to designate this tetragraptid.

The different direction of compression alters the aspect of this species very considerably. The distinctive characters cited before suffice however fully for its recognition in all cases. We have figured some of the more striking aspects. It appears that, on the whole, the branches of the Deep kill specimens are somewhat narrower, or at least do not reach the maximal width cited by Hall and Elles, while in all other respects, specially the length which they attain, they do not differ from the descriptions given by these authors.

In a paper on the growth and development of Goniograptus thureaui, the writer figured two extremely minute, apparently young specimens of a Tetragraptus, which he then thought referable to this species. Subsequent investigation has shown, that notwithstanding the resemblance between these and the mature specimens of T. similis, the young of the latter form are quite different, their siculae being larger and stouter, and not projecting below the first few thecae. As these minute rhabdosomes could not be referred to any other species of Tetragraptus, they have been described as a new type (T. pygmaeus).

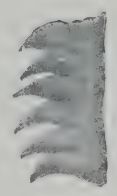

Fig. 61 Tetragraptus similis Hall *sp.* Fragment of branch enlarged to show the characteristic aspect of the thecae in the compressed condition. Deep kill. x4.5

Holm succeeded in isolating specimens of T. similis (bigsbyi) and thus elucidating the structure of the proximal parts. He also gives figures of a very young specimen, showing the "Didymograptus stage," i. e. the sicula, the left and right thecae and the connecting canal. Some of his instructive figures have been copied in the discussion of the genus.

The surfaces of graptolite bed 2 at the Deep kill are covered with growth stages of this species. These verify Holm's observations, so far as their flattened condition permits the study of their original structure. We figure several of these stages which exhibit important features [pl.12, fig.8–10]. Specially remarkable among them is the very long, extremely thin filamentary nema, which in one specimen [fig.10] is seen to end in a relatively large, thinly chitinous disk with a somewhat thickened central part.

Very frequently the two branches of one side alone are preserved [fig.58], whereby the fossil receives the appearance of a Didymograptus, of

the group of D. caduceus. The two forms have no doubt been frequently confused for this reason. The character of the thecae and the different width of the proximal parts of the rhabdosomes furnish however a ready means of distinction. Young colonies also frequently become so obliquely compressed that both pairs of branches fall into one plane, each pair forming a horseshoelike curve, and the primary thecae and sicula together become visible [pl.12, fig.4]. Older specimens are nearly always laterally compressed.

### Tetragraptus woodi sp. nov.

Plate 12, figures 1, 15, 16

Tetragraptus bigsbyi Ruedemann (*pars*). N. Y. State Paleontol. An. Rep't. 1902. p.556

*Description.* Primary disk unknown; nema very thin, filiform. Rhabdosome of small size (about 19 mm in length). Sicula conspicuous, about 1.7 mm long; first theca originating near the apex of the sicula, apparently of like character and direction of growth as in T. similis; first and second thecae forming two branches of the first order, which have a horizontal direction. Branches of the second order 17 to 19 mm long in their mature state, approximately straight or curving outward, directed obliquely upward, diverging under angles of 30° to 50°; mostly under 40° in the compressed state; widest at the base (2.2 mm), and diminishing regularly toward the distal end to 1.4 mm. Thecae about 16 in 10 mm in the proximal portion, and quite constantly 12 in the same space in the distal portion; curved, strongly inclined (about 50°); widening toward the aperture, twice as wide at aperture as at base; short (1.4 mm near base); twice as long as wide (in distal parts of branches); in contact one half to three fifths of their length; apertural margin approximately straight if fully exposed, but as a rule appearing curved and slightly oblique to the axis of the thecae in distal thecae, producing with the concave outer margin a recurved apertural denticle.

*Position and locality.* Found as the predominant form in a single surface of graptolite bed 2 at the Deep kill, associated with Goniograptus

perflexilis, Tetragraptus fruticosus, Didymograptus nitidus.

*Remarks.* This form agrees in the character of its thecae fully with T. (bigsbyi) similis and has therefore been first considered by the writer as a variety of that species. The constancy and importance of its differential characters, and the absence of transitional forms to T. similis are, however, sufficient evidence of the fixation of this type and of its specific value. It differs from T. similis principally by the greater length, straight direction, obliquely outward growth and regular tapering of the branches. In its central portion and the basal parts of the secondary branches it does not differ materially from T. similis. It, therefore, represents undoubtedly a further development of that species in a direction, however, different from that leading to Phyllograptus.

### Tetragraptus taraxacum Ruedemann

Plate 12, figures 17-26

Tetragraptus taraxacum nom. nud. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.589, fig.16

A small but very characteristic form, which is easily recognized among the multitude of species intermixed on the slabs of the Tetragraptus beds (graptolite bed no. 2).

*Description.* The sicula is middle sized and slender (1.3 to 1.7 mm). The two primary thecae, the first of which buds in about the middle of the sicula, are very long, cylindric (1 to 1.4 mm) and diverge at approximately right angles from the sicula. The four ultimate branches which spring from the same are gently curved upward to such an extent that they rise only a little above the apical end of the sicula. The angle of divergence between each pair of branches apparently amounted to as much as 180°. Their average length is 6 mm; greatest width 1.4 mm; greatest length observed 9.7 mm.

The first theca of each branch is still long and tubular and provided with a straight apertural margin as the primary thecae; the following thecae assume rapidly a very different aspect by widening strongly toward the

aperture and increasing in overlap. Their outer margins are strongly concave and the apertural margins protracted, convex and recurving, giving the distal thecae, in a lateral view, a bluntly cuspidate aspect. The mature thecae are three times as wide at the aperture as at the initial point; the overlap increases within each branch from one fourth to a little more than one half. There are 12 thecae in 10 mm, the outer margins of which at the beginning of the branch form an angle of 4° and at the distal parts an angle of 40° to 60° with the axis of the branch. The angle between the apertural margin and the axis of the branch is about 60°.

*Position and localities.* The majority of the specimens have been obtained in graptolite bed 2, of the Deep kill section, belonging to the Tetragraptus zone; a few were also observed in the beds with Diplograptus dentatus at Mt Moreno, near Hudson N. Y. The species appears hence to range through several zones.

*Remarks.* This type is remarkable for the long slender shape of the earlier thecae of the rhabdosome and the abrupt change to more curved and more closely arranged thecae, which are provided with protracted apertures and form a greater angle of divergence with the axis of the branch. The latter change is consequent on the closer arrangement and greater overlap of the thecae. This abrupt change in the shape and arrangement of the thecae appears as an interesting illustration of acceleration of development in the ontogeny of the branches [1902, p.589], the transitional stages between the earlier and mature thecae being here omitted. This feature, the small size of the rhabdosomes and the gentle curvature of the branches will easily distinguish it from the other congeners.

### Tetragraptus pygmaeus sp. nov.

Plate 12, figures 11-14

Tetragraptus bigsbyi Ruedemann (*pars*). N. Y. State Paleontol. An. Rep't. 1902. p.590, fig.18

In a former paper [1902, p.590] the author of the present memoir has referred minute tetragraptids, occurring in considerable number in graptolite

bed 2 of the Deep kill section, on account of their general similarity in early growth stages, to T. bigsbyi Hall. Subsequent, more detailed investigations, and specially a close comparison of these supposed growth stages with the proximal ends of T. bigsbyi, described by Holm, have demonstrated the error of this reference and the fact that these pygmies among the graptolites represent a species of their own, which differs in important characters from the other congeners.

*Description.* Primary disk chitinous, subcircular, of small proportions [fig.13, about 1 mm in diameter]; nema of varying length [fig.11]; sicula relatively long (1.4 mm) and slender (width at aperture but .3 mm), with long apertural spines; projecting beyond the branches of the first order by one fourth or more of its length; branches of first order monothecal, diverging perpendicularly from the sicula, about .6 mm long; each producing by dichotomy two branches of the second order, the latter reclined; subparallel to the sicula, very small (maximal length observed but 2.7 mm). Thecae very minute, numbering 18 in 10 mm, short, twice as wide as long; gradually ascending (initial angle about 30°); strongly curving outward in the distal parts (80° to 90°), at the aperture twice as wide as at the base. Outer margin strongly concave; apertural margin slightly concave, provided with acute apertural denticles, which on the two primary thecae appear to develop into spines.

*Position and localities.* Quite common in the graptolite bed 2 (belonging to the Tetragraptus zone); also rarely observed in graptolite bed 3, on slabs with Didymograptus bifidus and Goniograptus geometricus and in the beds with Diplograptus dentatus at Mt Moreno, near Hudson N. Y.

*Remarks.* This species is apparently related to T. (bigsbyi) similis, with which it agrees in the general form of rhabdosome and thecae. It can be distinguished from growth stages of that larger type by the smallness of its thecae, slenderness and protrusion of the sicula beyond the primary branches and the acute denticles of the thecae.

### Tetragraptus (Etagraptus) lentus sp. nov.

Plate 9, figures 7-10

*Description.* Sicula large (2.1mm) and slender. Primary theca generally budding from the first third of the sicula, this and the next forming right angles with it; narrow, tubular and long (1.6). Secondary branches at first forming obtuse angles, generally about 120°, with the primary branches, but later on assuming positions perpendicular to them. Branches narrow and flexuous, maximal width .37 mm, total length not known. Thecae extremely long (attaining a length of 2.4 mm), tubular and slightly curved; seven times as long as wide, little widening toward the aperture; overlapping not more than one fourth of their length, numbering 6 in 10 mm. Outer wall subparallel to the axis of the branch, forming an angle not surpassing 5° with the latter. Apertural margin straight and perpendicular to the axis of the branch.

*Position and localities.* Graptolite bed 3 at the Deep kill. On slab with Didymograptus bifidus and Goniograptus geometricus.

*Remarks.* There is no similar form known to the writer which would invite comparison. Coenograptus gracilis, while readily distinguished by the arrangement of the branches, has very similar thecae and branches. The direction of the secondary branches is in this species the same as in Tetragraptus approximatus Nicholson, which, however, is entirely different in the character of sicula and thecae.

### DIDYMOGRAPTUS McCoy

The genus Didymograptus was proposed by McCoy [1851, p.9] for uniserial forms, which are bifid from the base. Later Hopkinson separated the forms with solid axes in the branches under the generic term Dicellograptus.

We have in the introduction attempted to trace the genetic relationship of the species of Didymograptus, described in this publication, to forms with a greater number of branches; and there discussed the fact that the various Didymograptidae represent the biramous development of different

series of originally multiramous forms. The genus is hence like Tetragraptus polyphyletic and expresses a stage reached nearly simultaneously along many lines of evolution. It, accordingly, falls naturally into groups which probably unite species of actual genetic relationship. These groups have, through the larger and more varied association of British Didymograptidae, recently been determined by the monographers of the fauna of that country. They have, again, by common characteristics of general habit, been arranged into series. These are based largely on the divergence of the branches, which compasses the entire circumference of a circle [*see* diagram, p.485], probably in consequence of the endeavors of the branches to assume progressively a more and more erect position from the point of suspension (the sicula). We have adopted here for the arrangement of our species of Didymograptus the grouping proposed by Elles and Wood.

Group 1 Type: D. extensus
- D. extensus
- D. nitidus
- D. patulus
- D. similis
- D. gracilis

} Horizontal series

Group 2 Not represented

Group 3 Type: D. affinis
- D. ellesi
- D. acutidens
- D. cuspidatus
- D. nicholsoni var. planus
- D. filiformis
- D. törnquisti
- D. spinosus

} Declined series

Group 4 Not represented

Group 5 Type: D. murchisoni
- *a* Subgroup of D. bifidus
- D. bifidus
- *b* Subgroup of D. indentus
- D. nanus

} Dependent series

Group 6 Not represented

Group 7 Type: D. caduceus
D. caduceus
D. caduceus var. nanus
D. forcipiformis
D. incertus
} Reclined series

### Didymograptus extensus Hall sp.

Plate 13, figures 17, 18; plate 14, figures 1-4

Graptolithus extensus Hall. Geol. Sur. Can. Rep't. 1858. p.132

Graptolithus extensus Hall. Canadian Organic Remains, decade 2. 1865. p.80, pl.2, fig.11–16

Graptolithus constrictus Hall (pars). *Ibid.* p.76, pl.1, fig 23–27

Didymograptus extensus Nicholson. Ann. and Mag. Nat. Hist. ser. 4. 1870. 4:341, pl.7, fig.2, 2a

Didymograptus extensus Hopkinson & Lapworth. Quar. Jour. Geol. Soc. 1875. 31:642, pl.33, fig.1a–1d

?Graptolites (Didymograptus) extensus McCoy. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 2. 1875. p.29, pl 20, fig.1, 1a

Cf. Didymograptus constrictus Linnarsson. 1879

Didymograptus extensus Brögger. Die sil. Etagen 2 and 3. 1882. p.40

Cf. Didymograptus constrictus Brögger. *Ibid.* 1882

Didymograptus extensus Herrmann. Geol. Mag. Dec. 3, 1886. 3:14

Cf. Didymograptus constrictus Herrmann. *Ibid*

Didymograptus extensus Lapworth. Roy. Soc. Can. Proc. and Trans. 1887. 4:168, 184

Didymograptus extensus Ami. Geol. Sur. Can. Rep't, ser.2. 1889. v.3, pt2, p.116k

Cf. Didymograptus constrictus Ami. *Ibid*

Didymograptus extensus Roemer-Frech. Lethaea palaeozoica. 1897. 1:591

Didymograptus extensus Elles. Quar. Jour. Geol. Soc. 1898. 54:504

Didymograptus extensus Törnquist. Lunds Univ. Årsskrift 1901. Bd 37, Af.2, Nr 5, p.14, pl.1, fig.25–30

Cf. Didymograptus constrictus Törnquist. *Ibid.* p.17, pl.2, fig.13–17

Didymograptus extensus Elles & Wood. Monogr. Brit. Grapt. pt1. Pal. Soc. vol. for 1901. p.8, pl.1, fig.1a, b

Didymograptus extensus Ruedemann. N.Y. State Paleontol. An. Rep't. 1902. p.556

*Description.* Primary disk subcircular, relatively large (diameter 5 mm where the rhabdosome has a length of 6.5 mm), nema short, filiform, very thin. Sicula inconspicuous, short (1.3 mm) and relatively broad. Branches horizontal, angle of divergence 180°; attaining great length (incomplete specimens measure upward of 40 cm), increasing very gradually in width from .7 mm to 2.4 mm; slightly flexuous. Thecae 9 in 10 mm; short and broad (proportion of length to width, 2:1 in the proximal portion and 3:1 in the distal portion), attaining a length of 2.2 mm in the distal part; in contact for one half of their length in the proximal and two thirds in the distal parts; inclined at an angle of 35° to 40°. Outer and apertural margins straight, the latter normal to the axis of the theca (inclined at 130° to the axis of branch).

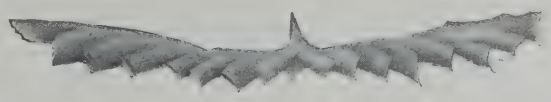

Fig. 62 Didymograptus extensus Hall *sp.* Proximal part of rhabdosome. Reverse view. Deep kill. x5.25

*Position and localities.* At the Deep kill this species has been found only in graptolite bed 2 (Upper Tetragraptus zone), where it, in association with Tetragraptus similis, covers one layer and in others is very common and associated with Dichograptus octobrachiatus, Tetragraptus fruticosus and Phyllograptus ilicifolius. Hall obtained his types from the Quebec group at Point Levis (Tetragraptus zone); Lapworth records it also from the zone with Phyllograptus anna, citing as locality "3 miles above St Anne"; and Ami lists D. extensus from several localities in the neighborhood of Levis. In Great Britain it has been recognized in the Middle Skiddaw slates of the Lake district; in the St David's district and the Lleyn peninsula of Wales (Hick's Lower Arenig); in Shropshire; and in the Ballantrae district in Scotland. Brögger records it from the Phyllograptus shale of the Christiania region; Törnquist found it in the zone of Isograptus gibberulus (lowest zone of his Phyllo-Tetragraptus beds) of Scania; and Frech mentions it also from the Hunneberg in

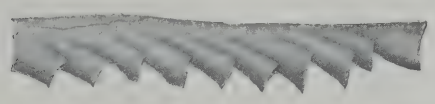

Fig. 63 Didymograptus extensus Hall *sp.* Fragment of proximal part of branch. Deep kill. x5.25

Westrogothia. It is not reported from the Bohemian, Belgian and French graptolite beds. McCoy identified a graptolite, which he found abundantly in Victoria, with this species, but his description and figures indicate a somewhat closer arrangement and a greater inclination of the thecae. In Europe the form is restricted to the lower Phyllograptus shale, corresponding to the Tetragraptus zone of the Deep kill, in which it also in America finds its principal development; but, according to Lapworth, it passes here also into the next higher zone with D. bifidus and Phyllograptus anna.

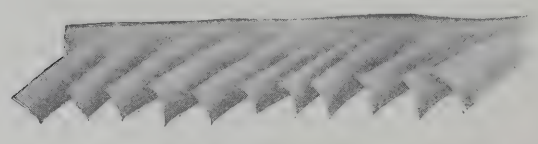

Fig. 64 Didymograptus extensus Hall *sp.* Fragment of mature part of branch. Deep kill. x5.25

*Remarks.* D. extensus can, in the material from the Deep kill, be readily distinguished from its congeners by the great length and nearly uniform width of the branches and its relatively broad thecae. In this representative the genus Didymograptus attained here its maximal development; for individuals like that figured on plate 14 [fig.1] may have reached 1 m in length. Also in final width the Deep kill examples of the species pass considerably beyond the maxima observed elsewhere.

Intermingled with typical specimens of D. extensus occur numerous others which have the appearance of those figured on plate 13 [fig.17, 18]. They are as a rule more flexuous, have a uniform width (about 1.9 mm) throughout their length, and possess a constrictiform appearance of the thecae. As these are the principal characters of Hall's species D. constrictus, we have no doubt that the latter species is based on specimens which became compressed in a certain direction, namely obliquely dorsolaterally instead of laterally, so that the frontal or apertural side of the thecae is partly exhibited. On this account Hall found also that the "common body occupies a very small proportion of the entire width, and its limits are not distinctly defined." The common canal lies in this mode of preservation behind the exposed side. The

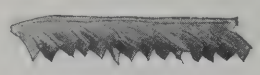

Fig. 65 Constrictiform appearance of a branch of Didymograptus. Deep kill. x2

sicula also is either covered entirely or only exposed with its apex, as in figures 17, 18 of plate 13.

As Hall states that the types of D. constrictus have been associated with D. patulus, it is possible that they may in part at least, represent the constrictiform mode of preservation of that species. The forms, identified by other authors with D. constrictus Hall, may be based on the constrictiform appearance of still other species.

### Didymograptus nitidus Hall sp.

Plate 13, figures 1-5; plate 14, figures 5, 6

Graptolithus nitidus Hall. Geol. Sur. Can. Rep't for 1857. p.129

Graptolithus nitidus Hall. Canadian Organic Remains, decade 2. 1865. p 69, pl.1, fig.1–9

Didymograptus nitidus Nicholson (*pars*). Quar. Jour. Geol. Soc. 1868. 24:135

Non Didymograptus nitidus Nicholson. Ann. and Mag. Nat. Hist. ser.4. 1870. v.5, p.342, fig.3a-c

?Didymograptus nitidus Etheridge jr. Ann. and Mag. Nat. Hist. ser.4. 1874. 14:6, pl.3, fig.20

Didymograptus nitidus Herrmann. Geol Mag. Dec. 3, 1886. 3:15

Didymograptus nitidus Barrois. Ann. de la Soc. Géol. du Nord. 1892. t.20, p.91

Didymograptus nitidus Matthew. Roy. Soc. Can. Proc. and Trans. 1893. 11:114

Didymograptus nitidus Elles (*pars*). Quar. Jour. Geol. Soc. 1896. 54:499–502; p.500, fig.19; p.501, fig.20

Didymograptus nitidus Gurley. Jour. Geol. 1896. 4:295

Didymograptus nitidus Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1901. p.10, pl.1, fig.2a-c

Didymograptus nitidus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.554, 556

*Description.* Primary disk small (diameter about 3 mm), subcircular, tenuously chitinous, with a central node from which the short, thin nema proceeds. Sicula broad and short (about 1.3 mm long), branches diverging in their proximal parts under angles varying between 100° and 180° to a dis-

tance of 4 to 5 mm, then assuming a horizontal direction; widening gradually to a maximal width of 2.4 mm (average but 1.6 mm), attaining each a maximal length of 124 mm. Thecae closely arranged (11 to 13 in 10 mm), slightly curved, inclined to the axis at an angle of about 40°; three times as long as wide, in contact for two thirds or less in the proximal and for three fourths of their length in the mature portion of the branch. Apertural margin slightly concave, normal on axis of thecae (forming angle of 130° with axis of branch).

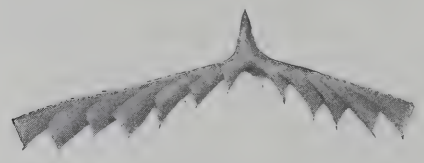

Fig. 65 Didymograptus nitidus Hall *sp.* Proximal part of rhabdosome. Reverse view. Deep kill. x6

*Position and localities.* At the Deep kill this species has been found to be restricted to graptolite beds 1 and 2, which represent the Tetragraptus zone. In these it is quite common. Hall reports it from the shales of the Quebec group at Point Levis. As at the latter point the Tetragraptus zone and the zone with Diplograptus dentatus are represented, and the association with species from the latter zone is always carefully mentioned, it is to be inferred that Hall's types were associated with the major fauna, that of the Tetragraptus zone. Strangely enough Ami [1889, p.116k], Lapworth [1886, p.184] and Gurley [1896, p.295] do not cite this species as having been found in the collections of graptolites of the Quebec group, which they investigated. Lapworth's material did not contain representatives of the Tetragraptus zone; and in Ami's lists it has most probably been referred to D. extensus, to which it is most similar. Matthew cites this species from horizon 3d of the St John group in New Brunswick. In Great Britain the form is widely distributed in the Middle Skiddaw slates of the Lake district,

Fig. 67 Didymograptus nitidus Hall *sp.* idem. Shows point of origin of first theca and growth lines. Deep kill. x5.25

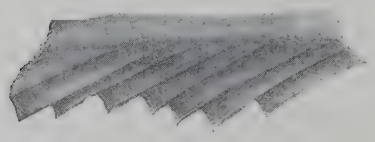

Fig. 68 Didymograptus nitidus Hall *sp.* Distal part of branch. Deep kill. x5.25

corresponding to the Tetragraptus beds of the Deep kill, in the Middle Arenig of St David's, in the Lleyn peninsula of Wales and in Shropshire. In Scandinavia the species does not appear to have as yet been clearly recognized; Herrmann [*loc. cit.*] cites it as "doubtfully in Phyllograptus shales, Norway." Barrois describes D. nitidus as common in the graptolite schists at Boutoury near Cabrières; and the younger Etheridge records it from Castlemaine in Victoria, Australia, but his identification is doubted by Lapworth, Elles and Wood.

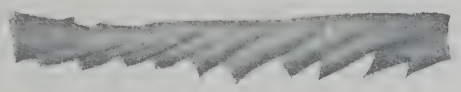

Fig. 69 Didymograptus nitidus Hall *sp.* Fragment of branch, showing different aspects of thecae due to different direction of compression. Deep kill. x5.25

*Remarks.* The primary disk is observable in a considerable number of specimens. It is found close to the apex of the sicula, so that the latter appears to have been as a rule attached by only a very short nema and even without the intercalation of such, as in figure 3. I have not observed any disks on larger rhabdosomes, but this is possibly due to the fact that I did not find any larger specimens so isolated and unencumbered by other fossils on smooth surfaces that I was able to distinguish these delicate appendages.

This species approaches D. patulus on one hand, and D. extensus on the other, and it is difficult to assign some forms to one of the three. This is specially true in regard to the differentiation of the closely allied species D. nitidus and D. patulus. The closer arrangement of the thecae in D. nitidus and the greater width of the branches of D. patulus are the principal distinctive characters. The greater number of thecae within a certain space and the more rapid widening of the branches will also distinguish the typical D. nitidus from D. extensus.

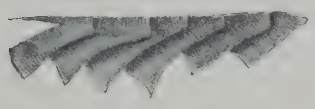

Fig. 70 Didymograptus nitidus Hall *sp.* Fragment of branch. The periderm is lost and the form of the coenosarcal cavities is shown by the pyrite filling. Deep kill. x7

A few of the specimens which we had to refer to this species [fig. 5] greatly surpass in length and width of the branches attained the examples described from Canada and Great Britain. At the same time they show just a little looser arrangement (11 in 10mm) than the typical D. nitidus, but still a greater number of thecae in a unit than D. extensus and D.

patulus. As the form of the thecae does not permit a reference to either of the two last named species, the one having broader and shorter, the other more inclined and curved thecae, it has been with us a question of either creating a new specific term or extending the definition of D. nitidus sufficiently to include these forms. We have preferred the latter, as the two are connected by such easy gradations that it would be impossible sharply to divide them. As, however, in other localities the species is evidently restricted to its typical expression, the fact of the variation calls for recognition, and we propose to designate these larger forms with somewhat less closely arranged thecae as the variety D. nitidus var. grandis.

### Didymograptus patulus Hall *sp.*

Plate 13, figures 8, 9; plate 14, figure 7

Graptolithus patulus Hall. Geol. Sur. Can. Rep't for 1857. 1858. p.131

Graptolithus patulus Hall. Canadian Organic Remains, decade 2. 1865. p.71, pl.1, fig.10–15

Non Didymograptus patulus Nicholson. Quar. Jour. Geol. Soc. 1868. 24:135

Non Didymograptus patulus Nicholson (*pars*). Ann. and Mag. Nat. Hist. ser.4. 1870. 5:340, pl.7, fig.1a

Didymograptus patulus Hopkinson. Quar. Jour. Geol. Soc. 1875. 31:644, pl.33, fig.4a-e

Didymograptus patulus Linnarsson. Sver. Geol. Und. Afh. och Upps. 1879. ser.C, no.31, p.5

Didymograptus patulus Brögger. Die sil. Etagen 2 and 3. 1882. p.39

Didymograptus patulus Herrmann (*pars*). Geol. Mag. Dec. 3, 1886. 3:14

Didymograptus patulus Matthew. Royal Soc. Can. Proc. and Trans. 1893. 10:98

Didymograptus patulus Matthew. Royal Soc. Can. Proc. and Trans. 1894. 11:114

Didymograptus patulus Gurley. Jour. Geol. 1896. 4:295

Non Didymograptus patulus Elles. Quar. Jour. Geol. Soc. 1898. 54:504, fig.22, 23

Non Didymograptus patulus Törnquist. Lunds Univ. Årsskrift. 1901. Bd 37, Af.2, Nr 5, p.15, pl.2, fig.1–6

Didymograptus patulus Elles & Wood. Monogr. Brit. Grapt. pt1. Pal. Soc. vol. for 1901. p.13, pl.1, fig.8a–c

Didymograptus patulus Ruedemann. N.Y. State Paleontol. An. Rep't. 1902. p.556

*Description.* Primary disk large, subcircular, very tenuous [fig. 9]. Nema very short (.3 mm) or absent [fig. 9]. Sicula inconspicuous, about 2 mm long. The first theca originates a little above the middle of the sicula, the second near its aperture. The branches horizontal, nearly straight, attaining a length of 5 cm and more, narrow in the proximal part (.7 mm), but widening rather rapidly to a maximal width of 2.6 mm and narrowing again at the growing end. Thecae numbering 10 to 12 in 10 mm, curved and inclined at 40° in their proximal and 60° in their distal part, four times as long as wide, in contact two thirds to three fourths of their length. Outer margin distinctly concave, apertural margin straight to slightly concave, mucronate at the lower end, forming an angle of 40° to 50° with the axis of the thecae.

Fig. 71 Didymograptus patulus Hall *sp.* Young rhabdosome. Obverse view. Deep kill. x 5.25

*Position and localities.* D. patulus is at the Deep kill very common in graptolite beds 1 and 2, representing the Tetragraptus zone, but apparently does not persist to the zone with D. bifidus. Hall received his type from the Quebec group at Point Levis. Gurley records it from the Main Point Levis zone, which corresponds to our Tetragraptus zone. Ami does not mention it in his list, but Matthew found it to be common in association with D. nitidus in division 3d of the St John group.

In England other species have, as Lapworth, Elles and Wood assert, been repeatedly mistaken for this type. According to these authors, it occurs in the Lower Llanvirn beds of the St David's district in Wales, associated with D. bifidus, D. nicholsoni, etc.; in the Middle and Upper Arenig of the Shelve district in Shropshire; and at Kiltrea near Ennisworthy in Ireland. It appears, hence, in Great Britain, to find its principal development in a higher horizon than in America. In the Skiddaw slates it seems to

be absent. Brögger cites it from the Phyllograptus shale of Krekling in the region of Christiana (according to Herrmann Lower Phyllograptus shale), and Herrmann adds Scania and West Gothland. Törnquist's identification of this species among the forms from the last named provinces is however not recognized by the monographers of the English graptolite fauna, and its occurrence in Sweden is hence still doubtful.

*Remarks.* The reference list of the species shows distinctly by the number of erroneous identifications cited how difficult of exact recognition this form is. The writer's experience verifies this fact; for, while in the lower graptolite beds of the Deep kill a majority of the specimens readily suggest by their habit that they might belong to this species, a comparison by measurements, with the types and the data given by Hall, brings out the fact that nearly all specimens oscillate in their characters between the typical D. patulus and D. nitidus. Hall states that the former species differs from the latter "in the greater extent of the stipes, and in their almost lineal character" and adds: "The form of the denticles and their angle with the axis, as well as their proportional distance, are distinctive characters." Our material contains specimens of D. nitidus with stipes that are longer and as straight as those of D. patulus. The graptolites, here referred to D. patulus, have wider and more rapidly widening branches, more inclined and curved thecae with mucronate apertural margins, but the thecae exhibit constantly a somewhat closer arrangement than Hall has recorded for D. patulus, and at the same time they are not so closely arranged as in D. nitidus. Our forms have also more rapidly expanding branches which attain a greater width than either Hall's or the English types.

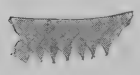

Fig. 72 Didymograptus patulus Hall *sp.* Fragment of branch. Deep kill. x2

Hall stated, further, that the inclination of the thecae in D. patulus is 60°; the thecae of our material have an initial inclination of 40°, which however increases to 60° toward the aperture. The drawings of Hall's types exhibit the same degree of curvature of the outer margin of the thecae.

Lapworth, Elles and Wood also comment on the resemblance of D. patulus and D nitidus, specially in the proximal region, and cite

the smaller number of thecae in a unit of length and the general absence of curvature in the branches of D. patulus as distinctive characters. Their specimens of the latter species have a looser arrangement than ours (9 to 10 in 10 mm), while the thecae in the drawings [p.14] do not exhibit the curvature and inclination described by Hall as characteristic of that species.

These facts indicate that there is a considerable number of varieties grouping themselves around and between the typical forms of D. patulus and D. nitidus.

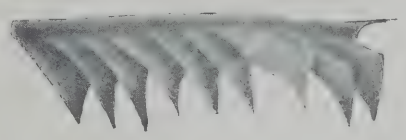

Fig. 73 Didymograptus patulus Hall *sp.* Fragment of distal portion of branch. Deep kill. x 5.25

We have observed a primary disk which in the specimen figured [fig. 9] is subcircular, fairly well outlined, has a diameter of about 12 mm and though showing but a trace of carbonaceous substance, is distinctly set off from the surrounding surface by its smoothness and depressed margin. Like the primary disks of other forms, it possesses in the center a small, somewhat more projecting circular portion. The apex of the sicula lies upon the apex of this projection and was hence evidently fastened to the disk either by a very short nema or without the intercalation of one. Since in hundreds of otherwise perfect specimens of D. patulus the sicula shows no trace of a nema, I feel satisfied that this species was closely attached to the primary disk, and not suspended by means of a long nema as D. (gibberulus) caduceus.

### Didymograptus similis Hall *sp.*

Plate 14, figures 25–29

Didymograptus similis Hall. Canadian Organic Remains decade 2. 1865. p.78, pl.2, fig.1–5

Didymograptus similis Gurley. Jour. Geol. 1896. 4:295

Didymograptus similis Ruedemann. N.Y. State Paleontol. An. Rep't. 1902. p.566, 567

*Description.* Nema and primary disk not observed. Sicula small and inconspicuous, about 1.8 mm long. Branches diverging at 180°, maximal length attained unknown (longest fragment observed 45 mm); widening

rapidly from .8 mm in the proximal part to the maximal width (about 1.8 mm), which is maintained. First and second thecae originate near the apex of sicula. Thecae numbering 9 to 10 in 10 mm, relatively short and wide tubes; width one third to one half of the length; inclined at an angle of about 30°, their outer margin straight or slightly concave, free for one third to one fourth of their length; apertural margin straight, forming with the axis of branch an angle of about 120° (normal on axis of theca).

Fig. 73 Didymograptus similis Hall *sp.* Very early growth stage of rhabdosome. Obverse view. Shows sicula and first thecae. Deep kill x5

*Position and localities.* Common in graptolite beds 3 and 5 of the Deep kill section (zone with D. bifidus) and very rare in the beds transitional from this zone to that with Diplograptus dentatus, on Mt Moreno near Hudson. The originals of the species were also taken from the same zone (Phyllograptus anna zone), three miles above the St Anne river in Canada. The form has not been reported from other localities.

*Remarks.* This species, which seems in America to be restricted to the zone with Phyllograptus anna and D. bifidus, has, on account of its short and broad thecae, been compared by Hall with D. sagittarius from the Normanskill shales. With associated congeners it has little similarity, but reminds sometimes of young forms of D. extensus, from which it can be distinguished by the less closely arranged and somewhat differently shaped thecae. It is however extremely similar to the Swedish species D. suecicus Tullberg and D. decens Törnquist. From the careful descriptions of the former species published by Tullberg [1880, p.43] and by Törnquist [1901; p.13], and of the latter by Törnquist [1891, p.18] it can be inferred that D. similis tallies in all important characters and completely in the measurements with these two forms; for their angle of divergence is 180°, number of thecae 9 to 10 in 10 mm, the angle of inclination 30°. Also the form and length of the sicula and the form of the thecae are

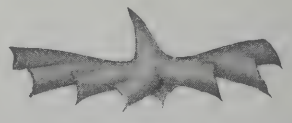

Fig. 74 Didymograptus similis Hall *sp.* Young rhabdosome. Reverse view. Deep kill. x6.5

alike. D. suecicus and D. decens are hardly to be distinguished from each other. Professor Törnquist, the author of the latter species, doubts himself whether they are really distinct and mentions the apparent occurrence of transitional forms. The facts, that D. suecicus has overlapping thecae which widen more toward the aperture, and that their outer margins are distinctly curved and free for but one third, are cited as affording distinctive characters. If we accept these differences as of specific value, D. suecicus will have to be regarded either as a vicarious form of D. similis or, I believe, as really identical with the latter and D. decens as a very closely related form. Tullberg held his D. suecicus to be nearly related to D. nitidus Hall. The latter differs, however, essentially in the rate of widening of the branches and specially in the much closer arrangement of the thecae.

D. suecicus occurs, according to Törnquist, abundantly in the third zone of the Phyllo-Tetragraptus beds (zone with Phyllograptus densus), and more sparingly in the second zone (zone with D. balticus). Hence it holds there about the same level in the lower graptolite shales as D. similis in America and is a member of a corresponding faunule.

### Didymograptus gracilis Törnquist

Plate 14, figures 15-21

Didymograptus gracilis Törnquist. Undersökningar öfver Siljansområdets Graptoliter I (Aftryck ur Lunds Univ. Årsskrift. Tom. 26). 1891. p.17, pl.1, fig.9–12

Didymograptus gracilis Holm. Geol. Fören. Stockh. Förh. Bd 17, H 3, 1895. pl.1, fig.7, 8

Didymograptus gracilis Elles. Quar. Jour. Geol. Soc. 1895. 54:506

Didymograptus gracilis Elles & Wood. Monogr. Brit. Grapt. pt1. 1901. p.24, pl.2, fig.2

Didymograptus (Leptograptus) sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep. 1902. p.589, fig.17

Non Graptolites (Didymograptus) gracilis McCoy. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 2. 1875. p.35

In the base of graptolite bed 3, the lowest outcrop of the zone with D. bifidus, several specimens of an extremely delicate Didymograptus were collected. These differ in no way from a species first noticed in Sweden. We give here a translation of the original description of the species.

From an almost uniformly thick sicula of 1 mm in length the two branches diverge at distinctly different hights, the one almost from the middle, the other from the upper end. Above these points of divergence the aperture of the sicula runs obliquely upward, so that it projects with a triangular tooth beyond the upper branch. The branches are of uniform width, .2 to .3 mm wide, and diverge almost at right angles from the sicula, but are irregularly bent in their continuation. Within a space of 10 mm 6 to 8 thecae are contained. These are long and narrow, with the periderm compressed, widening toward the aperture to about double the width. The outer wall of the thecae is slightly concave, sometimes almost straight; it forms a very acute angle with the dorsal margin. The apertural margin is perpendicular on the dorsal margin. Sometimes I believe I have seen a short internal canal. The length of the branches is unknown, but was certainly 15 to 20 mm and probably more.

Occurs in Phyllograptus shale at Skattungbyn. Fragments of branches are very common upon certain shales.

To this careful description we need only to add in way of enlargement that the branches are horizontal in their proximal part for the length of about three thecae and then mostly become gently reclined, a feature also apparent in Törnquist's drawings, or become flaccid; that the thecae are three to eight times as long as wide, their slenderness increasing distally, where the greater part of the thecae appears as a very gradually widening, hair-fine tube; and that the angle of inclination of the thecae is not more than 5° in the mature portion of the branches.

*Position and localities.* This species is not infrequent in graptolite bed 3 (the base of zone with D. bifidus[1]), where it is associated with Goniograptus geometricus and D. nanus, and it has also been found to occur still rarely in the beds at Mt Moreno, which contain a fauna transitional from this zone to that with Diplograptus dentatus. Törnquist

[1] In the *Report of the State Paleontologist* for 1901, p.556, this form has, as D. (Leptograptus) sp., been erroneously cited from graptolite bed 2.

describes it from the Phyllograptus shales of Skattungbyn in Dalarne, Sweden.

*Remarks.* This is by all means the most delicate and most attenuated species of Didymograptus which we have noticed in the New York fauna or found recorded from other regions. The tendency toward the development of long slender thecae and narrow flaccid branches, which appears first in Goniograptus perflexilis, has here apparently reached its most typical expression and also its termination. The distal portions of the rhabdosomes are frequently so fine that they are barely noticeable with the naked eye, and the lithographer did not produce these in their actual thinness for fear the lines could not be printed. The enlargement gives a better idea of this slenderest of all graptolites.

It has been stated in the preliminary paper on the Deep kill fauna, cited above, that the earlier thecae of this form are considerably shorter than the later ones (text p.533), and the phylogenetic significance of this feature has been pointed out. It was considered as indicating derivation of the species of Didymograptus with long, narrow thecae from forms with shorter and broader thecae. The same difference in the thecae is shown on figure 11 of Tullberg's drawings. In the Deep kill material the earlier thecae have a length of but .8 mm, while the later ones attain 2 mm in length. These are six to eight times as long as wide and appear tubular for two thirds of their length. The more proximal thecae, however, agree well with the enlargement given by Tullberg.

While our specimens, in the slenderness of the mature branches, the long tubular character of the thecae, their small overlap and inclination, seem to represent an extreme development of the characters described by Törnquist, or rather go beyond the typical Swedish form in development, the form referred to this species in England has more rapidly widening thecae and a correspondingly greater angle of inclination than the Swedish type and varies hence in the opposite direction to that of the Deep kill form.

### Didymograptus ellesi sp. nov.

Plate 14, figures 22-24

Didymograptus (Leptograptus) sp. nov. (*pars*) Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.589.

*Description.* Primary disk and nema not observed. Sicula relatively long, attaining a length of 1.2 mm, slender, very conspicuous [fig.23] on account of the slender character of the rhabdosome. Point of gemmation of first and second thecae not observed, that of the first theca apparently in the apical half of the sicula. Branches originating near the aperture of the sicula at different levels of the same, but slightly curved, of somewhat rigid appearance, slightly declined (angle of divergence quite uniformly 170°), very thin, very gradually widening from a proximal width not quite .2 mm to one of .4 mm; attaining a length of 14 mm or more. Thecae very slender, widening but very little toward the aperture, numbering 10 to 12 in 10 mm; three times as long as wide, inclined at an angle of 8° to 10°; overlapping about one eighth

Fig. 75 Didymograptus ellesi sp. nov. Sicula and part of one branch. Obverse view. Deep kill. x7

Fig. 76 Didymograptus ellesi sp. nov. Enlargement of a branch of the specimen reproduced on pl. 14, fig. 22. Deep kill. x6

of their length, the outer or apertural margins straight, the latter perpendicular on the axis of the theca.

*Position and locality.* Found on a single surface at the base of bed 3 at the Deep Kill, associated with D. nanus and D. gracilis.

*Remarks.* This form is readily distinguished from the associated, similarly delicate D. gracilis by the more rigid expression and uniform, slightly declined direction of the branches. Its nearest relations are clearly with D. affinis Nicholson among the types of Didymograptus and with Bryograptus lapworthi, here described, among the older multiramous forms

From the former it differs by the somewhat closer arrangement of the thecae and their smaller angle of inclination. To the latter it bears such a remarkable similarity of habit that a genetic connection of the two can not be gainsaid [p.557].

### **Didymograptus acutidens** (Lapworth ms. em. Elles & Wood)

Plate 13, figure 15

Didymograptus affinis Hopkinson. Quar. Jour. Geol. Soc. 1875. v.31, pl 33, fig.6b,c

Didymograptus acutidens (Lapworth ms em. Elles & Wood). Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1901. p.25, pl.2, fig.3a–d

*Description.* Only one specimen of this species has been observed. This presents the following characters. Primary disk and nema not present. Sicula slender, about 1.2 mm long, branches originate at slightly different levels, the first theca curving away from a point about two thirds the length of the sicula from its apex and the second theca nearer to the aperture. Mature length of branches not observed, branches diverging at an angle of 180°; straight, but not rigidly so, very slender, .4 mm wide in the proximal portion and attaining a width of .6 mm. Thecae numbering 11 in 10 mm, four times as long as wide, in contact for one third to one half of their length; inclination 15°. Outer margin straight; apertural margin concave with a denticle.

Fig. 77 Didymograptus acutidens L.,E. &W. Proximal portion of rhabdosome. Obverse view. Deep kill. x5

*Position and localities.* A single specimen has been found on a slab with Phyllograptus anna, Dichograptus octobrachiatus, etc., belonging to the lower part of the zone with D. bifidus. In Great Britain the same species occurs, according to the monograph of the British graptolite fauna, in the Lower Llanvirn of the St David's district in Wales and of south Shropshire; hence at about the same level as on this side of the Atlantic.

*Remarks.* This form is in its habit so similar to Bryograptus lapworthi, described above, that, having but one specimen, I would not

have ventured to describe it as belonging to a different species. The fact however, that this specimen occurs in a zone where Bryograptus lapworthi has become extinct, and that it agrees still more closely with a species of Didymograptus occurring in the same zone in Great Britain, justifies the identification. From Bryograptus lapworthi the specimen differs by the somewhat closer arrangement of the thecae, the more prominent denticulations of the apertural margins and the greater angle of divergence of the branches.

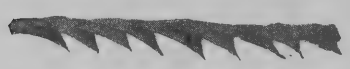

Fig. 78 Didymograptus acutidens L., E. & W. Fragment of branch. Deep kill. x5

### Didymograptus cuspidatus sp. nov.

Plate 13, figure 16

*Description.* The single specimen of this species observed presents the following characters. Primary disk and nema not present. Sicula short, apparently not longer than .8 mm, and inconspicuous. Branches originate suborally, at slightly different levels; diverge at first at an angle of 140°, and become later subhorizontal. Length of mature branches has not been observed; their width is at first very small (.4 mm), but increases rapidly to the double dimension. Thecae number 11 to 12 in 10 mm, are slender (three times as long as wide in the proximal portion of the branch), but rapidly become wider, their apertural width being in later thecae one half the length; they are hardly in contact in the early portion of the branch and overlap later to about one third to one half of their length. The inclination of the early thecae is only about 18°; it increases to about 40° in the apertural part of the later thecae. The latter is characteristically prominent, giving the thecae a cuspidate appearance; the outer margin is straight in the proximal portion of the thecae and concave in the apertural; the apertural margin slightly convex in the outer and concave in the inner part; on the whole appearing straight and vertical on the axis of the thecae.

Fig. 79 Didymograptus cuspidatus sp. nov. Proximal portion of rhabdosome. Ash hill quarry at Mount Moreno. x5

*Position and locality.* In the shales with Diplograptus dentatus at Mt Moreno near Hudson.

*Remarks.* This species is nearest related to D. acutidens Lapworth, of which it presents the characteristic features in a further developed stage. As it also succeeds the latter in geologic time, it may well be considered as a descendant of it. It differs from D. acutidens most markedly in the prominence of the apertural portion of the thecae, which in most thecae appears cuspidate instead of acutely dentate, as in D. acutidens. This is due to a widening, often somewhat abrupt, of the thecae in their last growth stage.

Fig. 80 Didymograptus cuspidatus sp. nov. Fragment of branch. Ashhill quarry at Mt Moreno. x5

## **Didymograptus nicholsoni** Lapworth
## var. **planus** Elles & Wood

Plate 13, figures 10-14

Didymograptus nicholsoni var. planus Elles & Wood. Monogr. Brit. Grapt. pt1. Pal. Soc. vol. for 1901. p.29, pl.2, fig.5a, b

*Description.* Primary disk and nema unknown. Sicula small (about 1.6 mm long), relatively broad. Branches straight, or very slightly curved, of rigid appearance, both together forming a straight line (angle of divergence 180°); short (maximal length observed 28 mm); narrow, of nearly uniform width (about 1.1 mm) after the sixth theca (width in proximal part .5 mm). Thecae numbering 10 to 11 in 10 mm, narrow, four times as long as wide, inclined at 20°, in contact for but one fourth to one third of their length. Outer margins straight. Apertural margins slightly concave, normal on axis of theca; two thirds the width of the branch.

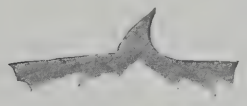

Fig. 81 Didymograptus nicholsoni Lapw. *var.* planus E. & W. Proximal portion of rhabdosome. Obverse view. Deep kill. x7

Fig. 82 Didymograptus nicholsoni Lapw. *var.* planus E. & W. Fragment of branch. Deep kill. x7

*Position and localities.* Rare in graptolite bed 2 (Tetragraptus zone); associated on slabs with Tetragraptus fruticosus, T. similis, T. pygmaeus and Dichograptus octobrachiatus. The authors of the variety report it from the Upper Skiddaw slates of Outerside in the Lake district of North England.

*Remarks.* I have hesitated for some time to identify my material with the variety from the Skiddaw slates, for the reason that the latter has thus far

Fig. 83 Didymograptus nicholsoni Lapw. *var.* planus E. & W. Proximal portion of rhabdosome. Reverse view. Deep kill. x4

been found in a higher horizon; but I have failed to find any important distinguishing characters, and the branches and thecae appear to agree with the British types in all details. The somewhat smaller figures for the size of the sicula in our material may be due to an incomplete preservation of the apical end. The branches appear to originate in our specimens [*see* figure 81] very close to the apex of the sicula and diverge from the latter suborally.

### Didymograptus filiformis Tullberg

Plate 14, figures 8-14

Didymograptus filiformis Tullberg. Geol. Fören. Stockh. Förh. 1880. 5:42, pl.2, fig.8-11

Didymograptus filiformis Lapworth. Ann. and Mag. Nat. Hist. ser. 5. 1880. 6:20

Didymograptus filiformis Brögger. Die sil. Etagen 2 and 3. 1882. p.39

Didymograptus filiformis Tullberg. Sver. Geol. Und. 1882. Afh. och upps. ser.C, no. 50. p.22

Didymograptus filiformis Törnquist. Lunds Univ. Årsskrift, Bd 37, Af 2. nr. 5. 1901. pl.3, fig.6-9

Didymograptus cf. filiformis Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. 1901. p.32, fig.20

Didymograptus filiformis Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556

There occur in the uppermost part of graptolite bed 2, belonging to the Tetragraptus zone, very minute and delicate rhabdosomes of a type of the declined group of Didymograptus, which is sufficiently close in its specific characters to a species described by Tullberg to warrant identification with it.

*Description.* The sicula is small (1 mm) and narrow. The first and second thecae branch out at different distances from the apex of the sicula. The rhabdosome is hence distinctly unsymmetric regarding the origin of the branches. The latter are rather short, if complete and of uniform width (not exceeding .25 mm). The largest branch measures only 3.2 mm in length. The angle of divergence between the two branches is about 60° to 80°; in one specimen 110°, probably by oblique compression. The thecae are very slender, tubular, hardly widening, numbering 8 in 10 mm, inclined at only 10° to 15° and overlapping not more than one quarter of their length. The outer walls and the apertural margins are straight; and the angle which the latter form with the axis of the branch is 90° or more.

These characters, which are constant in about half a dozen specimens, differ slightly from the original description of Tullberg, who observed an inclination of the thecae of about 30°. But Tullberg's figures show an angle of inclination not larger than the one observed in the Deep kill specimens, and the English specimens furnished also a smaller angle.

*Position and localities.* It has been collected in the uppermost part of graptolite bed 2 (Tetragraptus zone), associated with the sicula of all the other species, with which it probably settled at the same time on account of its similar weight and size. A few specimens were also observed in the beds with Diplograptus dentatus at Mt Moreno near Hudson N. Y. The range of this species is hence considerable. Tullberg obtained the type of the species from the lower Graptolite shales of Kiviks-Esperöd in Scania, and cites it later (1882) as a form of the Tetragraptus zone of Scania. Törnquist found it at Mossebo in Westrogothia; and Brögger in Etage 3b (Phyllograptus-schiefer) at Krekling in Norway. Elles and Wood record that their material has been collected in the Arenig rocks of Bennane Head near Ballantrae, Scotland.

### Didymograptus törnquisti sp. nov.

Plate 13, figures 6, 7

*Description.* Primary disk unknown; nema present. Sicula small (1.2 mm). The point of origin of the first theca has not been distinctly observed. The branches diverge near the apertural end of the sicula, are nearly horizontal, gently curved, attaining their full width (1.1 mm) near the proximal part and maintaining it. Thecae numbering 8 in 10 mm, inclined at an angle of about 20°, three times as long as wide, in contact about one third of their length. Outer and apertural margins straight, the latter normal on direction of axis of theca.

*Position and locality.* In graptolite bed 3 (zone of D. bifidus) associated with Goniograptus geometricus, Tetragraptus pendens, D. bifidus and D. similis.

*Remarks.* Only one specimen of this species has been observed. Its principal characters, viz the loose arrangement and low inclination of the thecae and the small amount of overlap, distinguish it from other forms except D. affinis Nich., which however has much narrower branches and a shorter sicula. From the similar D. nicholsoni var. planus, which occurs in the underlying bed, it differs by the smaller number of thecae in a unit length.

### Didymograptus spinosus sp. nov.

Plate 14, figures 30-32

*Description.* Primary disk and nema not observed. Sicula small and little conspicuous (.9 mm). First thecae diverging suborally. Branches moderately deflexed, their angle of divergence about 120°; very thin at the beginning (not .3 mm wide), but widening rather rapidly within 10 mm to 1 mm. Mature length and width of branches unknown; the longest branch observed attains a length of 16 mm. Thecae numbering 12 in 10 mm; narrow, four times as long as wide in the proximal and three times as long as wide in the more distal parts of the rhabdosome; inclined at 20°; in contact

for but one third of their length in mature parts of rhabdosome. Outer margins concave, apertural margins straight, normal on axis of theca; one half the width of branch; provided with long, straight spines, which have a direction perpendicular to the axis of the branch. The dorsal wall of the branches also provided with perpendicular spines, which alternate with the apertural ones.

Fig. 84 Didymograptus spinosus sp. nov. Proximal portion of branch. Ashhill quarry at Mount Moreno. x4.5

*Position and locality.* Rare in the shales with Diplograptus dentatus at Mt Moreno.

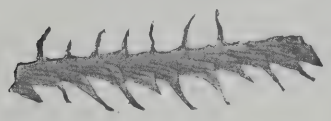

Fig. 85 Didymograptus spinosus sp. nov. Portion of distal part of branch. Ashhill quarry at Mount Moreno. x4

*Remarks.* This species is at once distinguished from all other forms of Didymograptus known to me, by its double row of spines. There has however been described a species of Tetragraptus (T. acanthonotus Gurley, 1896. p.65), from the Beekmantown shales at Point Levis, which exhibits the same spinous dorsal margin as the species in hand, and which may indicate the line of descent of this Didymograptus [p.558].

### **Didymograptus bifidus** Hall sp.

Plate 15, figures 1-3

Graptolithus bifidus Hall. Canadian Organic Remains, decade 2. 1865. p.73, pl.1, fig.16-18; pl.3, fig.9, 10

Didymograptus bifidus Nicholson. Quar. Jour. Geol. Soc. 1868. 24:136

Didymograptus bifidus Nicholson. Ann. and Mag. Nat. Hist. ser. 4. 1870. 5:346, fig.7

Didymograptus bifidus Hopkinson & Lapworth. Quar. Jour. Geol. Soc. 1875. 31:646, pl.33, fig.8a-e

Didymograptus bifidus (?) Brögger. Die sil. Etagen 2 and 3, etc. 1882. p.41

Didymograptus bifidus Herrmann. Geol. Mag. ser. 3. 1886. 3:15

Didymograptus bifidus Ami. Geol. Sur. Can. Rep't, ser. 2. 1889. v.3, pt2, p.116k

Didymograptus bifidus Barrois. Ann. de la Soc. Gèol. du Nord. 1892. 20:92

Didymograptus bifidus Gurley. Jour. Geol. 1896. 4:295

Didymograptus bifidus Elles. Quar. Jour. Géol. Soc. 1898. 54:511

Didymograptus bifidus Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1901. p.42, fig.26a and b

Didymograptus bifidus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.566, 567

*Description.* Nema and primary disk not observed. Sicula long and slender, about 2 mm long. Branches dependent, rounded at their base, then straight; angle of divergence of first thecae 90° to 100°, that of branches mostly varying between 20° and 25°; the branches attaining a length of 26 mm, expanding gradually to a maximal width of 2.4 mm near the distal growing ends, the latter showing a rapid contraction. Thecae closely arranged, numbering 13 to 15 in 10 mm, inclined at an angle of 45° in the mature and of about 30° in the proximal parts; two to three times as long as wide; in contact for one half of their length in the proximal and three fourths in the mature parts. Apertural margin slightly concave, forming an angle of 135° with axis of branch.

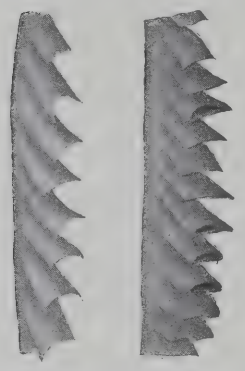

Fig. 86 Didymograptus bifidus Hall *sp.* Portions of rhabdosomes enlarged to show the form of the thecae. Deep kill. x5.25

*Position and localities.* In the Deep kill section common, but restricted to graptolite beds 3 to 5, which represent the zone with Phyllograptus anna and D. bifidus. Hall records it from Point Levis and from a point 3 miles above the river St Anne; Gurley lists it [1896] as a fossil of the Phyllograptus anna zone (St Anne zone), and also as occurring in the Upper Levis zone (zone with Diplograptus dentatus, etc.), from which it is absent at the Deep kill. He reports it further from Nevada [*ibid.* p.304]. According to Ami the species occurs in various localities in the province of Quebec [1889, p.116k]. In Great Britain this species is, according to Lapworth, Elles and Wood, "more common than any other member of the dependent series; it occurs in great numbers at one particular horizon, namely, in the Upper Arenig beds below the zone of D. murchisoni". It is cited there from various localities in Ireland, Scotland, Eng-

land (Lake district and Shropshire) and Wales. Brögger identified a form of the middle part of the Phyllograptus shale of the neighborhood of Christiania, with some doubt, with D. bifidus; and Herrmann cites this as a somewhat divergent form from Norway. In Scania (Sweden) it occurs in the Phyllograptus typus zone, associated with the same faunule as in America. In Bohemia it is found, according to Perner, in D 1$\gamma$, associated with a great number of other dependent forms. Barrois reports it as a common fossil in the schists with Bellerophon oehlerti at Boutoury near Cabrières, in the Languedoc. The species has not yet, to my knowledge, been found in Australia, nor have the other dependent forms been announced from there; and it is therefore probable that the zones characterized by these forms have not yet been met with. It can be inferred from its general distribution that it, while characteristic and best developed in the zone which we have named after it, also extends into the next higher zone in various regions.

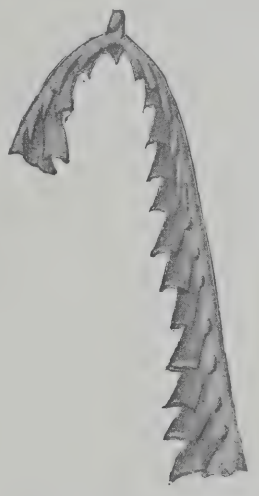

Fig. 87 Didymograptus bifidus Hall *sp.* Shows the "pustules," the common canal and the thickened apertures. Deep kill. x7

*Remarks.* This widely distributed species is the type around which group themselves the dependent species of Didymograptus, most of which it precedes. It has been carefully described by several writers, lastly by the monographers of the British graptolites. The latter observed that two groups or types of forms could be recognized by the angle of divergence, that both, however, are connected by a long series of intermediate forms. We have noticed only one of these groups, i. e., the one with a small angle of divergence. This is also the more common form in Great Britain.

One of our specimens [text fig.87] in which the common canal and the first theca were pyritized, shows that the latter originated about midway between the apex and aperture of the sicula, grew a short distance along the sicula and then turned to one side. The second theca appears to originate at or near the geniculation of the first theca.

The same specimen throws also some light on a peculiar feature which is most noticeable in D. bifidus, namely the presence of small pustules at the bases of the thecal walls. These were also noticed by Hall.[1] They are not always present; hence an accidental feature. When present they are situated with great regularity at the place mentioned. This fact and their composition of iron pyrite indicate that they originate by crystallization of pyrite in the basal rings, which, as Perner's sections of specimens of Monograptus [*loc. cit.* pl.1, his *renflements piriformes à l'extrémité des ouvertures internes*] show, were formed by the pyriform swelling of the interior ends of the thecal walls. This ring held open, while the perisarc was being compressed, a small, vacant space sufficiently long for the commencement of the formation of the pyrite nodules.

### Didymograptus nanus Lapworth

Plate 15, figures 4, 5

Didymograpsus geminus Nicholson. Quar. Jour. Geol. Soc. 1868. 24:134, pl.5, fig.8, 9

Didymograpsus geminus Nicholson (*pars*). Ann. and Mag. Nat. Hist. ser. 4. 1870. 5:346, fig.6b

Didymograptus indentus var. nanus Lapworth. Quar. Jour. Geol. Soc. 1875. 31:647, pl.33, fig.7d; pl.35, fig.4a-c

Didymograptus indentus var. nanus Elles. Quar. Jour. Geol. Soc. 1898. 54:511

Didymograptus nanus Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1901. p.47, pl.4, fig.5a-h

*Description.* Nema and primary disk not observed. Sicula slender, full length not observed. Branches attaining a length of 22 mm or more, slender, of uniform width (1.3 mm), angle of divergence approaching at first 90° but soon becoming about 12° or less. Thecae numbering 10 to 12 in 10 mm, inclined at 30°, rather long and narrow (ratio of length to width 3:1), in contact for one half of their length in the mature portion of the branch. Aper-

[1] *See* his figures, pl.1, fig.18 and pl.3, fig.10. In the explanation of the latter figure they are specially mentioned.

tural margin normal on the axis of theca (forming an angle of 150° with axis of branch).

*Position and localities.* A single surface in the quarry beds (graptolite bed 5, belonging to the zone with D. bifidus) was found to contain this species in numerous specimens. The species has not been reported from Canada. In Great Britain it occurs in the Upper Arenig of the St David's and Lake districts (Middle and Upper Skiddaw slates), in association with D. bifidus and Diplograptus dentatus.

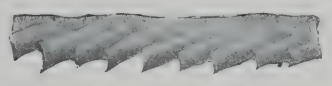

Fig. 88 Didymograptus nanus Lapworth. Portion of branch. Deep kill. x5.5

*Remarks.* This form was originally described by Lapworth as a dwarf variety of D. indentus Hall (*recte* dentatus; *see* Frech, *Lethaea palaeozoica* 1:590), with which it agrees in everything except size and number of thecae in a given unit of length. While it is sufficiently distinct to be recognized as a species, its close relationship to D. dentatus Hall is undubitable.

Brögger [*loc. cit.* p.40] records the occurrence of a variety of D. dentatus at Krekling near Christiania. This may also be a D. nanus.

### **Didymograptus (Isograptus) caduceus** Salter *emend.* Ruedemann

Plate 15, figures 6, 7

Didymograpsus caduceus Salter (*pars*). Quar. Jour. Geol. Soc. 1853. 9:87, fig.1a

Didymograpsus caduceus Salter (*pars*). Quar. Jour. Geol. Soc. 1863. 19:138, p.137, fig.13a

Graptolites (Didymograpsus) caduceus McCoy. Pal. Geol. Sur. Victoria. Prodr. Pal. Victoria, decade 2. 1874. p.30, pl.20. fig.3–5a

Tetragraptus bryonoides Hall (D. caduceus Salter) Etheridge jr. Ann. and Mag. Nat. Hist. ser.4. 1874. 14:2, pl.3, fig.3, 4

Didymograptus gibberulus Nicholson. Ann. and Mag. Nat. Hist. ser.4. 1875. 16:271, pl.7, fig.3, 3a, 3b

Phyllograptus stella Hopkinson. Quar. Jour. Geol. Soc. 1875. 31:658, pl.34, fig.6

Didymograptus gibberulus Moberg. Geol. Fören. Stockh. Förh. 1891. 13:221

Isograptus gibberulus Moberg. Geol. Fören. Stockh. Förh. 1892. 14:346, pl.8, fig.3–7

Didymograptus gibberulus Holm. Sver. Geol. Und. Afh. och upps. 1895. ser.C, no.150, p.18

Didymograptus (Isograptus) gibberulus Römer & Frech. Lethaea palaeozoica. 1897. 1:593, fig.161

Didymograptus gibberulus Elles. Quar. Jour. Geol. Soc. 1898. 54:496

Isograptus gibberulus Törnquist. Lunds Univ. Årsskrift. 1901. Bd37, Afd.2, p.23, pl.3, fig.16–19

Didymograptus gibberulus Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1901. p.52; p.53, fig.33a and b, pl.2, fig.9a-9e

*Description.* Primary disk not observed. Nema filamentous, very thin and long. Sicula long and slender (length about 3.2 mm). Two branches which, bending in opposite directions upward and slightly backward, form a rhabdosome of horseshoe shape; the angle of divergence of the branches varying, in the material, between 300° and 330°. The branches are short (greatest length observed 5.6 mm); widest at their base (about 2.2 mm) and diminishing in width toward the distal ends to one half their original width, this diminution being produced by a change in the direction of the thecae from straight downward to obliquely outward and upward. Thecae long (the proximal ones about 2 mm long) numbering 11 to 14 in 10 mm, slightly curving with the convex side upward, inclined in their distal part toward the axis at an angle of 45°, three times as long as wide, in contact throughout. Apertural margin concave, mucronate at the lower end and receding upward.

*Position and localities.* At the Deep kill this form has been obtained only in half a dozen specimens found on a slab which was picked up loose at the outcrop of graptolite horizon 2 (zone with D. bifidus). I have not been able to locate the bedding surface which is covered with this interesting form, but, from the lithologic aspect of the slab, I believe that it came from the eastern part of the quarry (graptolite beds 5), which in some parts is little accessible now. Numerous specimens of a much dwarfed mutation of this species [cited 1902, p.570, as D. (Isograptus) gibberulus Nich. var. nanus var. nov.] were found in graptolite bed 7 (horizon with

Diplograptus dentatus). They will be described in addition to this species.

In northern Europe this species has been well known for a long time. In England it occurs in the Upper Tetragraptus beds of the Middle Skiddaw slates, hence in the equivalent of the horizon to which it probably belongs in the Deep kill section. It is also reported from the same horizon in the shale of the St David's district in Wales (Phyllograptus stella Hopkinson). In Sweden it characterizes a horizon of the lower Graptolite shale of Scania and Westrogothia [Törnquist, *loc. cit.*]. Holm had isolated material from the Vaginatenkalk of Oeland. Frech mentions it as having been collected near Christiania by F. Roemer. It is also characteristic of the lower graptolite shales of Victoria [McCoy, Etheridge jr] and New Zealand, Australia [*fide* Frech]. It has not been recorded from the Bohemian basin.

Fig. 89 Didymograptus caduceus Salter. Young rhabdosome. Obverse view. Deep kill. x4.2

*Remarks.* This species of striking appearance and taxonomic importance has been elaborately described by Moberg, Elles, Törnquist and Lapworth, Elles and Wood. Our material is not sufficient to verify all the observations of these authors, specially in regard to the central parts of the rhabdosome, much less to add to their descriptions. We learn from these investigators that the first theca originates very near the apex of the sicula and follows the latter to a point near the aperture of the sicula, where it bends away from the latter. Also the second theca is nearly as long as the first, so that the connecting canal must lie very high up.

Moberg proposed to make this species the genotype of a new genus, Isograptus, on the ground that in this form the branches arise bilaterally symmetric from the sicula, and each branch is not itself bilaterally symmetric, while in Didymograptus both branches arise at somewhat different levels at the sicula, and each branch is itself bilaterally symmetric. Holm has however shown the relations of branches and sicula to be the same in Didymograptus

and Isograptus, and on this ground reunited this form with Didymograptus. Lapworth, Elles and Wood have pointed out later [*loc. cit.* p.53] that the observation made by Törnquist, that "the first stipe crosses the sicula and the second stipe the first theca," seems to indicate a deviation from the normal Didymograptus type of development, that is to say, a forecast of the type characteristic of the Diplograptidae, and that this, if substantiated, might afford grounds for the retention of this form as the type of a subgenus. But it seems to me that, without entering into the details of the initial parts, D. gibberulus differs in so important characters, that it clearly constitutes a separate group, which, when the polyphyletic origin of the genus Didymograptus shall be established, and the components of the various series be made out, will find recognition by a separate term. It represents the reclined group of forms, in which the branches grow straight upward, and the thecae are in contact throughout their length.

Nicholson has asserted that two very different forms had been thrown together by Salter under the term D. caduceus. He separated the biramous component as D. gibberulus, at the same time pointing out that this species can be readily distinguished from the other component, the similar preservation of Tetragraptus bigsbyi, where but two branches are preserved, by the fact that in D. gibberulus the rhabdosome is widest in its proximal part, while in Tetragraptus bigsbyi it is narrowest there [comp. pl.12, fig.6 and pl.15, fig.6]. Nevertheless, the two forms have probably been confused on more than one occasion, and D. caduceus may for this reason have a still wider distribution than is accorded to it.

If Salter indeed comprised two forms under one specific term, according to present usage, the form which he figured first has still to retain his name, and the other to be separated under a new name. The two forms now, which are thought to be united under Salter's term, viz D. gibberulus Nicholson and Tetragraptus bigsbyi Hall, bear indeed a superficial resemblance, when the latter is so preserved that but two branches are seen. But, as Nicholson, and later Elles have asserted, they can be readily distinguished by the aspect of the proximal part. Using this criterion, the reliability of which

we had occasion to verify in our material, in regard to Salter's figures, in combination with other characters, it must be concluded that Salter's first two drawings and his description [1853, p.87] can apply only to the form later on described as D. gibberulus by Nicholson. Of the two drawings comprised in a later publication [1863, p.137, fig.13a, 13b] under this name, the former is surely the Didymograptus, the latter represents probably a Tetragraptus bigsbyi. This conclusion is supporte dby the fact that a long nema is noticeable in the first two drawings and is also cited in the original description; for, while the species of D. gibberulus are notable for their long nema, one will not notice this filiform suspensory organ among hundreds of specimens of Tetragraptus bigsbyi.

It is, hence, apparent that Salter had before him, at the time of the original description of D. caduceus, the form which, later on, was described and is generally known as D. gibberulus Nicholson, a name which has, then, to give way to Salter's older name. Salter's specimens were obtained by Dr Bigsby from the "Lauzon Precipice," and came therefore from the Quebec shales. Hall had evidently no examples of this species in his material from the Quebec shales, or he would not have failed clearly to recognize the difference between his Tetragraptus bigsbyi and D. caduceus Salter. He states in regard to the former: "These forms resemble the Graptolithus caduceus of Salter which was obtained by Dr Bigsby from 'the Lauzon Precipice,' and I have hesitated in regard to making of them a new species." The writer has found D. (gibberulus) caduceus in the Deep kill shales, so that there can be no doubt of the presence of that species on this side of the Atlantic.

R. Etheridge jr figures both forms here discussed as Tetragraptus bryonoides, considering D. caduceus as a synonym of that species. It is clear, however, from his description, that he was aware of the constancy of the differences of the two forms, united by him under that name, and he suggests that Salter's name might be retained as a varietal designation for such forms as those shown by his figures 3 and 4, which represent specimens of D. gibberulus Nicholson.

There is, to state this difficult and confused relation of the various names more concisely, no doubt in our mind that D. caduceus Salter should have preference to Nicholson's later and better known name, D. gibberulus; that Salter's name can not be applied to Tetragraptus bigsbyi Hall, which name in its turn has to yield to the older name Tetragraptus similis Hall.

### Didymograptus caduceus Salter nanus mut. nov.

Plate 15, figures 8, 9

A small form, which I had cited in Museum bulletin 52, 1902, *loc. cit.* as D. gibberulus var. nanus, but which more correctly should be designated as D. caduceus mut. nanus, occurs quite frequently in the last horizon (graptolite bed 7, zone with Diplograptus dentatus). It differs from D. caduceus in its constantly smaller size (the largest specimen observed having a length of but 5 mm), its wider proximal part (2.3 to 2.5 mm), the abrupt narrowing of the branches [fig.8], the smaller size and closer arrangement of the thecae (14 to 18 in 10 mm), the distal convergence of the branches and the spinous processes of the lower ends of the apertural margins.

Fig. 90 Didymograptus caduceus Salter nanus mut. nov. Deep kill. x7

These characters clearly indicate a concentration of the entire development of the rhabdosomes into smaller space and shorter time, denoting the paracmic condition of the mutation. This concentration finds its most pregnant expression in the specimens, of which figure 90 is an example. In this the distal points of the two branches point toward each other and have approached so closely that the further gemmation of thecae appears impossible, and a further growth of the branches will consist only in the prolongation of the last thecae, which will produce the rapidly tapering branches of figure 8. The formation of long spines is a secondary character, acquired in this stage.

### Didymograptus forcipiformis sp. nov.

Plate 15, figures 10-13

*Description.* Primary disk not observed. Nema filamentous, extremely thin. Sicula long and slender (length about 3.6 mm). Two branches, bent at their bases to such a degree that their distal parts, which are straight, become subparallel (angle of divergence 350° or more); they attain a considerable length (24 mm), are wide at their bases (3 mm), but taper rapidly to a width of .6 mm or less. Thecae long in the basal part of the branches (3 mm), but becoming shorter in the distal portions, where they are more inclined (45°); numbering but 9 to 10 in 10 mm, curved, about three times as long as wide, in contact throughout their length. Apertural margin slightly concave, lower part produced into a mucro or short spine in the distal portion and into long spines in the long, proximal thecae.

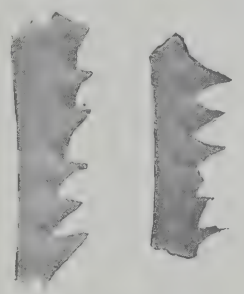

Fig. 91 Didymograptus forcipiformis sp. nov. Middle portion of branch. Ashhill quarry at Mount Moreno. x5

*Position and locality.* This species has been observed only in the beds with Diplograptus dentatus at Mt Moreno near Hudson, in one layer of which it occurs quite frequently.

*Remarks.* D. forcipiformis differs from D. caduceus Salter, of which it is a late derivative, by the greater divergence of the branches, by the smaller width of the distal portion of the branches and their greater rate of tapering, the great width of the proximal portion of the branches, the less close arrangement of the thecae and the presence of mucros or spines at the apertural margins.

Elles and Wood state that there occur among the British forms of D. gibberulus Nicholson (= D. caduceus *nobis*) several mutations, in one of which "the dorsal walls of the stipes are straight distally, the stipes running parallel to each other". Our form agrees with this mutation in the general direction of the branches, though the branches in D. forcipiformis approach each other still much more than they do in the examples figured by Elles. In fact, none of the European forms which I have seen figured appear

to show as closely approaching branches as the Mt Moreno form. The latter differs from all these still further by the looser arrangement of the thecae, which are provided with spines.

While this form does not possess the general gerontic aspect of the form designated in this work as D. caduceus mut. nanus, it appears as an extreme development of D. caduceus by the divergence and slenderness of the branches and has the spinous apertures in common with the paracmic mutation of D. caduceus, just cited.

### **Didymograptus incertus** sp. nov.

Plate 15, figure 14

Didymograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

*Description.* Primary disk and nema not observed. Sicula apparently rapidly tapering (longer than 1.5 mm). Branches reclined, first horizontally (about 2 mm), then diverging at an angle of 110°, their width in the proximal region about 1.2 mm, increasing to 1.9 mm and decreasing again toward the distal ends. Thecae numbering 8 to 9 in 10 mm, inclined at an angle of 40°, three times as long as wide, in contact for one half to two thirds of their length. Outer margin slightly convex, apertural margin concave, mucronate.

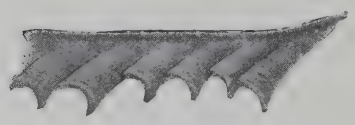

Fig. 92 Didymograptus incertus sp. nov. Portion of branch of specimen reproduced on pl.15, fig.14. Shows thickening of dorsal wall. Deep kill. x7

*Position and locality.* A single specimen was found in graptolite bed 7, horizon of Diplograptus dentatus; associated with the latter species, D. caduceus mut. nanus, etc.

*Remarks.* The sicula is preserved only fragmentarily and as an impression. Its characters, as well as those of the first theca could therefore not be made out with sufficient accuracy.

This form bears a superficial resemblance to D. caduceus and could be taken for a representative of that species, in which the branches have been

forced apart by some accident. Closer comparison shows however that the thecae are less closely arranged and free for a greater portion of their length.

The dorsal part of the common canal is so strongly thickened in this species that it appears like a solid rod, or virgula, suggesting in this feature, as in the general form, an approach to Dicellograptus.

## Family COENOGRAPTIDAE nom. nov.

### SIGMAGRAPTUS[1] gen. nov.

Two principal branches, which together form a sigmoidally curved rhabdosome. From these originate alternately on both sides, denticulate side branches which do not bifurcate again.

It is evident that this genus belongs to the coenograptids, its closest relationship being with Coenograptus itself, from which it differs only by the arrangement of the branches on both sides of the principal branches instead of on one side. It can however be noticed on well preserved specimens of Coenograptus gracilis that every second side branch bends across the principal stem to the same side as the preceding branch, so that the original arrangement of the branches of Coenograptus was probably the same as that in Sigmagraptus. As Coenograptus retains the sigmoid curve of the two principal branches and is a younger genus, it can be safely concluded that it is directly derived from Sigmagraptus. The species of Sigmagraptus, here described, has, as we have shown before, [p.565] a Goniograptus as ancestor.

The genus Pterograptus has the same alternating arrangement of the branches as Coenograptus, but they are there distinctly pendent and suggestive of a derivation from a Bryograptus with dependent branches. In Pleurograptus the branches are given off alternately on both sides as in Sigmagraptus but are provided again with tertiary branches. This structure could be readily referred to that of Sigmagraptus. The genus Amphigraptus, finally, which was erected by Lapworth [1873] for forms like Graptolithus divergens Hall, from the Quebec shales of Levis, is said to have the branches not

[1] *Sigma*, the letter *Sigma*, *grapho* to write.

arranged alternating but in pairs This genus has not been recognized by Roemer and Frech in the *Lethaea palaeozoica*, but has been united with Coenograptus. But, if the observation of the paired arrangement of the branches is correct, the mode of bifurcation must be essentially different from that in Coenograptus, Pterograptus etc. In fact, there is no other graptolite known to the writer in which a paired arrangement of side branches occurs.

All the other genera of the coenograptids (excluding Amphigraptus) appear much later than Sigmagraptus.

The stem or principal branch consists of thecae in exactly the same manner as that of Pterograptus and Coenograptus, i. e. each internode between two side branches is formed by one theca.

Genotype: Sigmagraptus praecursor sp. nov.

### Sigmagraptus praecursor sp. nov.

Plate 5, figure 13

Coenograptid gen. nov. et sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.566

The graceful slender branches of this species occur quite often in graptolite bed 3 of the Deep kill section. As, however, they are usually mingled in an intricate manner with specimens of Goniograptus and other ramifying species, it is difficult to observe perfect organisms. The example figured was found on a slab unobscured by other graptolites.

Fig. 93 Sigmagraptus praecursor sp. nov. Part of branch. Deep kill. x7

*Description.* Rhabdosome consisting of two principal stems, which together form a sigmoid curve. From these originate in regular intervals long, straight, filiform side branches, only .3 mm wide and which normally form angles of 90° with the principal branches. The latter have been seen to attain together a length of 40 mm, the side branches one of 20 mm. The sicula has not been found sufficiently well preserved for exact measurement; from it branch two primary thecae, with a length of 1.4 mm each, which form a horizontal central bar. The internodes between the branches consist of one

theca each and have a length of 1.8 mm each. The thecae are extremely slender, tubular, without any noticeable widening toward the aperture, overlapping about one third of their length; diverging from the axis of the branch not more than 12°; their outer walls and apertural margins are straight, the latter half as wide as the branch and forming an apertural angle of 5°. The brachial thecae number 8 in 10 mm.

*Position and locality.* Graptolite bed 3 of the Deep kill section, belonging to the zone with Didymograptus bifidus and Phyllograptus anna.

*Remarks.* The principal stems are found to be composed of thecae formed by the successive bifurcations. As alternately the right and the left of the two diverging thecae become internodes of the stem, the latter shows still an obscure zigzag line, suggestive of an origin identical with that of the principal stems of Goniograptus. While the mode of branching of Sigmagraptus, like that of the younger coenograptids, has to be designated as monopodial or lateral, one of the branches always essentially retaining the direction of the mother theca, still the faint presence of a zigzag curve in the principal stem indicates that the mode of branching in this form is also originally dichotomous in character, and differs only from that of Goniograptus in the greater degree of the divergence of the thecae, from which the denticulate branches originate, and a corresponding lesser degree of divergence of the stolonal or stem thecae.

No similar form, which would invite comparison, is known to the writer. Coenograptus gracilis, while easily distinguished by the arrangement of the branches, has very similar thecae and branches.

## Family PHYLLOGRAPTIDAE Lapworth

### PHYLLOGRAPTUS Hall. 1857

This genus was first defined by Hall in the report on Canadian graptolites [1857, p.31] and more fully described in his *Graptolites of the Quebec Group* [1865, p.118]. Hall recognized thus early the essential facts of its structure, viz the composition of the rhabdosome of four branches, which have coalesced

with their dorsal sides, but he considered the structure as analogous with that of Diplograptus, assuming that the fronds of the latter were formed by the coalescence of two monoprionidian branches, and as a corollary he inferred the presence of a solid axis or virgula as in Diplograptus. The rhabdosomes of

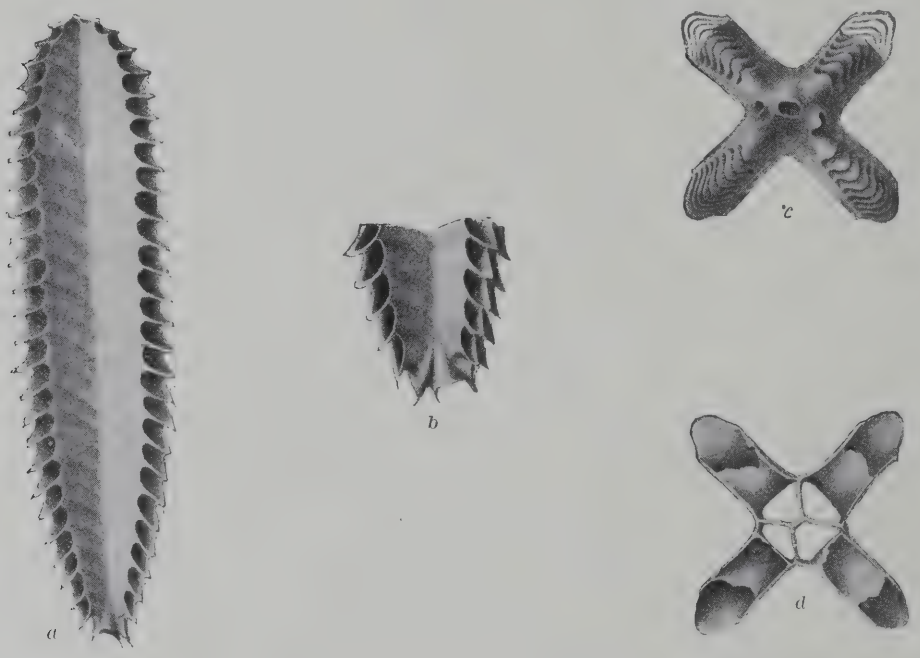


Fig. 94 Phyllograptus angustifolius Hall. *a* View of a rhabdosome, etched out of limestone. Seen from the reverse (antisicular) side. x4 *b* Sicular end of rhabdosome, seen from the obverse (sicular) side. x6 *c* Rhabdosome seen from the sicular end. Shows the apertures of the sicula (in the center), of the first two thecae (flanking the sicula), and of the earliest portions of the branches. x6. *d* Transverse section through a rhabdosome, showing the central coenosarcal canal and its four longitudinal septa. x6 (Copies from Holm)

Diplograptus have now however been demonstrated to be not the result of the coalescence of two branches, but of the budding of thecae of one series alternately on opposite sides. It is, hence, evident that the two genera are of entirely different structure. Subsequent observers, as Lapworth, Tullberg and Törnquist, have all corroborated Hall's conception of Phyllograptus, and Tullberg recognized the close relationship between Tetragraptus and Phyllograptus.

This relationship has now been fully demonstrated by Holm's fundamental work on the genera Didymograptus, Tetragraptus and Phyllograptus [1895, p.27]. Holm isolated specimens of P. angustifolius preserved plastically in the Vaginatenkalk of Oeland and by means of thin sections proved that the gemmation of the first thecae and the formation of the four branches of the rhabdosome take place in exactly the same manner as in Tetragraptus [text, p.476]. The sicula is embedded at the distal end of the rhabdosome, the four branches growing backward from the initial point toward the point of fixation, as in Tetragraptus (bigsbyi) similis. Between this species and P. angustifolius there exists the closest agreement, both in internal and external structure. In Phyllograptus, however, the four branches have coalesced, so that the four coenosarcal canals form a quadripartite internal tube, and the four independent periderm walls of Tetragraptus similis have united into "a single, cruciform, four winged, longitudinal septum" [section, fig.94*d*]. The longtitudinal partitions of the central tube consist, hence, of a single layer.

The material from the Deep kill consists largely of flattened specimens in slate. Among them there occur finely macerated examples in a layer of the quarry beds [pl.15, fig.33], which show the interthecal walls in excellent preservation. In a layer of graptolite bed 2 the specimens of P. ilicifolius were largely preserved plastically by having become the centers of pyrite nodules. Sections through these have permitted us to investigate the internal structure of that species.

Hall suggested that the fronds or rhabdosomes of Phyllograptus may have been attached in groups to some other support, a suggestion which was based on their arrangement on a slab figured on plate 15 (figure 10) of his work. This arrangement is, however, accidental, as the writer had occasion to satisfy himself, and, as is indicated by the irregular distribution of the antisicular extremities of the rhabdosomes. The mode of occurrence of Phyllograptus would rather suggest that the rhabdosomes as found now constituted the entire colony, only the organ of suspension having been lost or failed of preservation.

Holm states that no virgula has been observed [1895, p.489]; while Elles reports [1896, p.494] having seen one in a specimen of P. anna passing from the apical end of the sicula the full length of the rhabdosome. The homology of the structure with that of Tetragraptus similis argues certainly for the, at least temporary, suspension of the sicula from a primary disk by means of a nema. Corresponding to the growth of the four branches in a proximal (or backward) direction this nema must have become inclosed into the rhabdosome, analogous as in Diplograptus. If it then is sometimes absent, as Holm's observation in P. angustifolius would tend to show, it must have been received so intimately into one of the peridermal walls, that it is no longer distinguishable as a separate body, which is the more possible, as it is anyway an extremely slender and delicate thread in most Dichograptidae.

It is, however, a peculiar fact that among the very great number of well preserved specimens found in the New York shales not a single one has been observed with any trace of a nema protruding from the antisicular end of the rhabdosome. Nor do I find any suggestion in either the descriptions or the figures of other material indicating that such an organ has ever been noticed. Yet it is necessary to postulate the suspension of the colony from the ascending growth directions of the branches as well as of the thecae. The appendages, which were observed by Hall, in P. typus, and termed "radicles" are sicular spines and, therefore, found at the opposite free end of the rhabdosome. While we have not noticed them in our material of P. typus, they were found to be well developed in P. anna [pl.15, fig.23] and in P. ilicifolius.

The phylogeny of the group has been touched in the introduction [p.563].

### Phyllograptus ilicifolius Hall

Plate 15, figures 15-22

Phyllograptus ilicifolius Hall. Canadian Organic Remains, decade 2. 1865. p.121, pl.16, fig.1–10

Cf. Phyllograptus ilicifolius var. grandis Elles. Quar. Jour. Geol. Soc. 1898. 54:493

Cf. Phyllograptus ilicifolius var. grandis Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1902. p.102, pl.13, fig.8

Phyllograptus ilicifolius Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.554, 556.

*Description.* Rhabdosome consisting of four branches, mostly broadly semioval, which are joined at right angles by their longitudinal axes so as to form two intersecting ovals. The rhabdosome attains a maximum length of 19.5 mm and a width of 11.3 mm; the dimensions of average specimens are however smaller by one fourth. Character and length of sicula not ascertained; sicular end provided with a rather long (8 mm) spine. The thecae are in contact throughout their length, number, in the majority of the specimens, 12 in 10 mm, with variations to 11 and 13; they are much curved; first ascending near the sicular end, then curving outward and downward, this curvature decreasing gradually toward the center, where the thecae are but slightly bent and placed approximately horizontally; toward the antisicular portion of the rhabdosome they become more and more directed upward, till at the antisicular end they run subparallel to the axis of the rhabdosome. The apertures are slightly concave; oblique in the sicular portion and vertical on the axis of the thecae in the central and antisicular portions; their lower margins are extended into short concave tongues [fig.95] which in the laterally compressed rhabdosomes appear as slender mucros [fig.96].

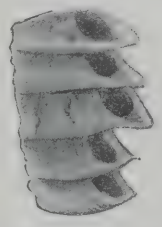

Fig. 95 Phyllograptus ilicifolius Hall. Marginal portion showing thecal apertures and mucros. Deep kill. x8

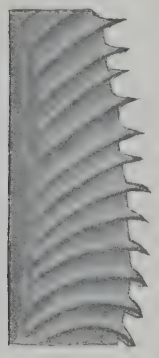

Fig. 96 Phyllograptus ilicifolius Hall. Enlargement of a part of a rhabdosome. Deep kill. x6

*Position and localities.* Very common and typical in graptolite bed 2 (Tetragraptus horizon); rare in graptolite bed 1, belonging to the same horizon and not observed in typical specimens in the highest horizon of the Deep kill section. In the beds with Didymograptus bifidus

it occurs still sparingly. Hall's types came from the first mentioned horizon. Elles and Wood describe from the Middle Skiddaw slates a varietal form as P. ilicifolius var. grandis, which differs from the typical material only by its much greater size. Some of the largest specimens from the Deep kill approach this major variety in form, but are connected by intervening sizes with the normal specimens.

*Remarks.* Hall described this form as broadly oval or ovate. While the majority of the numerous specimens in the Deep kill correspond to this description, there are on one hand extremely broad forms and on the other extremely long and narrow ones [fig.16, 19], transitional forms leading over to both extremes.

It is, hence, evident that in this bed at least P. ilicifolius is almost as variable as P. typus in a later horizon. The thecae in the middle part may approach the direction of those of P. angustifolius, but P. ilicifolius is always readily distinguished from that species by the direction of the thecae in the sicular and antisicular portions.

This form is also easily distinguished from P. typus, which follows it in the Deep kill section, by its more closely arranged thecae and the different character of the apertures, which here, in the compressed form, are adorned with long, narrow mucros.

### Phyllograptus typus Hall

Plate 15, figures 35-37

Phyllograptus typus Hall. Geol. Sur. Can. Rep't for 1857. 1858. p.137

Phyllograptus typus Billings. Geol. Sur. Can. Pal. Foss. 1865. 1:366,375

Phyllograptus typus Hall. Geol. Sur. Can. decade 2. 1865. p.119, pl.15, fig.1–12

Phyllograptus typus Törnquist. Lunds Univ. Årsskrift. T. 1, pt iii, 1865. p.16, pl.1, fig.9,10

Phyllograptus typus Nicholson. Quar. Jour. Geol. Soc. 1868. 24:133, pl.5, fig.16

Phyllograptus folium (His. sp.) var. typus (Hall) McCoy. Geol. Sur. Victoria. Prodr. Pal. Victoria decade 1. 1874. p.7f, pl.1, fig.1–4

Phyllograptus typus Brögger. Die sil. Etagen 2 and 3. 1882. p.41
Phyllograptus cf. typus Tullberg. Skånes Grapt. in Sver. Geol. Und. Afh. och upps. ser. C, no. 50. 1882. p.21
Phyllograptus typus Malaise. Ann. de la Soc. Géol. de Belg. 1888. t.15, bul. p.42
Phyllograptus typus Ami. Geol. Sur. Can. Rep't. 1889. v.3, pt 2, p.50k ff
Phyllograptus typus Gurley. Jour. Geol. 1896. 4:294
Phyllograptus typus Roemer & Frech. Lethaea palaeozoica. 1897. 1:605
Phyllograptus typus Elles. Quar. Jour. Geol. Soc. 1898. 54:494f
Phyllograptus cf. typus Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1902. p.99, pl.13, fig.5a,b
Phyllograptus typus Ruedemann. N. Y. State Paleontol. Ann. Rep't. 1902. p.566

This species, which, both by the gigantic size and the great variability of its individuals, marks the acmic stage of development in the short lived genus Phyllograptus has been fully described by its author. and lately by Elles and Wood. From these descriptions and the material in hand we derive the following enumeration of the distinctive features of the species.

*Description.* The rhabdosome is exceedingly variable in relative length and width, or in outline generally. Hall described it as being "elongate ovate or lanceolate, broad oval or obovate," and Miss Elles's extensive measurements demonstrate that in the Skiddaw specimens, the variations extend from long and narrow forms, whose relative length and width are 57 and 6.3 mm, to short and broad forms with 25.4 and 8.7 as corresponding figures. Our material does not quite reach these extremes, but still illustrates well the lack of fixation of the outline, and specially the frequent occurrence of lanceolate forms and the tendency of the rhabdosome to attain its maximal width in the sicular half.

The thecae are in contact throughout their length, number 9 to 10 in 10 mm, and are curved in all parts of the rhabdosome, viz in the sicular portion slightly upward, which curvature lessens toward the middle portion and finally assumes an obliquely upward direction in the antisicular portion. The apertures are but slightly mucronate.

The sicula has not been observed in any of the writer's specimens, nor has the sicular process, which according to Hall attains a length of about ½ inch, been noticed.

*Position and localities.* In the Deep kill P. typus has been found sparsely, in rather large specimens at the base of graptolite bed 3; and in great number, but in smaller size, in the intercalations in the quarry, belonging to the same zone (zone with Didymograptus bifidus).

According to its citations in the literature this species could be considered as one of the most widely distributed; it is, however probable that some of the graptolites which have been identified with it belong to other species. So for example, the monographers of the British graptolites have not been able to identify positively the material currently cited in Great Britain as belonging to P. typus with that Quebec species. And also in Sweden in later time, the investigators have not felt justified in doing more than to characterize the uppermost zone of the lower graptolite shale as the zone with P. cf. typus Hall. Gurley, further, refers with doubt a form from Arkansas to this species.

Hall's types came from the beds at Point Levis. As no associated forms are cited, it is uncertain whether these types were collected in the lower or upper Point Levis zone. From its associates in the Deep kill we suppose that this species belongs in the upper part of the lower horizon. Ami lists it from several localities near Point Levis, in association with forms of the Tetragraptus zone. Billings recorded it from the Cow head on Newfoundland. The specimens referred in Great Britain to the same are found in the upper beds of the Middle Skiddaw slates of the Lake district. Törnquist and Tullberg identify forms in Scania with it and Brögger mentions it as common in the shales at Christiania. It also has been collected by Cluysenaar and Lecrenier at Huy-Statte in Belgium and listed as Diplograpsus folium, the identification having been corrected by Malaise.

McCoy records it from numerous places in Victoria, Australia.

*Remarks.* According to Elles this species is characterized by (1) the number of thecae in a given unit of length, (2) the form of the aperture, which is equally extended at its upper and lower limits. These characters serve specially to distinguish the narrow variation of P. typus from P. angustifolius, which has more closely arranged thecae, and longer apertural mucros, which are extensions only of the lower part of the apertures giving the latter an oblique direction. Also, the character of the curvature of the thecae and, specially, the direction of those of the antisicular portion furnish a means of distinction of P. typus from P. angustifolius.

P. ilicifolius exhibits, in the Deep kill section, a variability of form similar to that of P. typus. It also possesses a similar character of curvature of the thecae, but has corresponding to its generally smaller size, more closely arranged thecae, and, besides, longer and differently shaped apertural mucros. P. typus and ilicifolius, though not mentioned by Hall as occurring in different associations are in their principal development, separated in the Deep kill section, where P. ilicifolius precedes P. typus.

### Phyllograptus angustifolius Hall

Plate 15, figures 31–34

Phyllograptus angustifolius Hall. Geol. Sur. Can. Rep't. for 1857. 1858. p.139

Phyllograptus angustifolius Salter. Quar. Jour. Geol. Soc. 1863. 19:137, fig.7a, b

Phyllograptus angustifolius Hall. Geol. Sur. Can. decade 2. 1865. p.125, pl.16, fig.17–21

Phyllograptus angustifolius Nicholson. Quar. Jour. Geol. Soc. 1868. 24:132

Phyllograptus angustifolius Linnarsson. Sver. Geol. Und. 1879. Afh. och upps. ser.C, no.31. p.5

Phyllograptus cf. angustifolius Tullberg. Sver. Geol. Und. 1882. Afh. och upps ser.C, no.50. p.22

Phyllograptus angustifolius Brögger. Die sil. Etagen 2 and 3. 1882. p.41
Phyllograptus angustifolius Ami. Geol. Sur. Can. Rep't. 1889. v.3, pt 2, p.50k ff
Phyllograptus angustifolius Holm. Geol. För. Förh. 1895. Band 17, heft 3, p.319, pl.3
Phyllograptus angustifolius Wiman. Geol. Inst. Upsala. Bul. 4. 1895. v.2, pt 2, p.39, pl.9, fig.8
Phyllograptus angustifolius Elles. Quar. Jour. Geol. Soc. 1898. 54:496
Phyllograptus angustifolius Elles & Wood. Monogr. Brit. Grapt. pt 1. Pal. Soc. vol. for 1902. p.100, pl.13, fig.7a-f
Phyllograptus angustifolius Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.554, 556, 570

Specimens referable to this species are found in all three horizons of the Deep kill section; the form does not however attain its typical expression till the third horizon (with Diplograptus dentatus), while the specimens of the first horizon (with Tetragraptus) approach P. ilicifolius and suggest a genetic connection between the two. The typical material possesses the following distinguishing characters.

*Description.* Rhabdosome consisting of four elongate, semielliptic branches, which have nearly equal width throughout or are a little wider near the sicular end. Thecae in contact throughout, numbering 11 to 13 in 10 mm, being very little curved and directed at a uniform angle obliquely upward, the inclination increasing somewhat toward the antisicular end. The thecae of the sicular end are in their proximal portion nearly horizontal and slightly bent down in their distal portion.

The apertures of this species are very characteristic, the mucronate extension of the lower part of the same being much longer than that of the upper, so that the margin of the aperture appears to recede in an upward direction. This extension attains a length of one and one half times the width of the thecae.

*Position and localities.* This species occurs in all three horizons of the Deep kill section. It finds its typical development in the last horizon (with

Diplograptus dentatus), specially in the lower part of the same, exposed in the Ashhill quarry at Mt Moreno, Hudson, where it is very common. Hall's types came from the shales of Point Levis; but, as no associated forms are mentioned, the horizon is not determinable from his data. Ami, however, cites it from several localities near Point Levis and Quebec in association with species of the zones of Didymograptus bifidus and of Tetragraptus. It can be thus inferred that, in the Quebec region as well as at the Deep kill, it ranges through several zones. A similar range of the species has been observed by Elles and Wood in Great Britain. Also in Sweden (Scania) it appears to be a form of the Tetragraptus horizon as well as of the Phyllograptus cf. typus zone. Brögger found it associated with P. typus and numerous varieties or mutations of the two species, in the upper beds of the Phyllograptus shale of Christiania. Holm obtained his material from the gray Orthoceras limestone of Oeland.

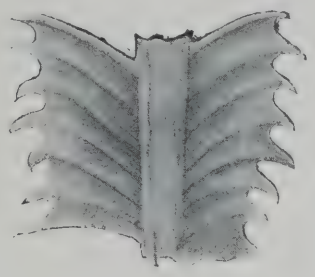

Fig.97 Phyllograptus angustifolius Hall. Middle portion of rhabdosome enlarged. Shows the shape of the apertures in compressed state, and the central canal. Deep kill. x4. 8

*Remarks.* While this species persists beyond the range of P. ilicifolius into the horizon with Diplograptus dentatus, it begins in the Tetragraptus beds, where P. ilicifolius is prevalent, with forms that possess the long linear outline of P. angustifolius and the uniform direction and curvature of the thecae in the middle portion, a characteristic that seems to be dependent on the narrow development of the rhabdosome, while in the antisicular part the thecae are still more ascending than in P. angustifolius, but not so strongly as in typical P. ilicifolius. The apertural mucros are not yet as strongly developed as in the P. angustifolius from the higher horizon, but of the same character, viz extensions of the lower margins. Indeed from a comparison of the drawings of the apertural extensions of P. angustifolius furnished by Holm [text fig.94] with those of P. ilicifolius [text fig. 95], it is to be inferred that they are of exactly the same character and differ

only in relative size. The form from the quarry beds appears to be transitional between the preceding older mutation, still closely related to P. ilicifolius, and the succeeding typical form in the uppermost horizon.

### Phyllograptus anna Hall

Plate 15, figures 23-30

Phyllograptus anna Hall. Canadian Organic Remains, decade 2. 1865. p.124, pl.16, fig.11–16

Phyllograptus anna Lapworth. Roy. Soc. Can. Proc. and Trans. 1886. 4:168

Phyllograptus anna Ami. Geol. Sur. Can. Rep't, ser. 2. 1889. v.3, pt 2, p.116k

Phyllograptus anna Gurley. Jour. Geol. 1896. 4:294

Phyllograptus anna Elles. Quar. Jour. Geol. Soc. 1898. 54:494, fig.16

Phyllograptus anna Elles & Wood. Monogr. Brit. Grapt. Pal. Soc. vol. for 1902. p.101, pl.13, fig.6a–f

Phyllograptus anna Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.566, 571

*Description.* Rhabdosome small, a single very large specimen attaining 13 mm, while ordinarily large specimens measure only 8 and 9 mm in length; the maximal width of the largest specimen was found to be 5.2 mm; branches broadly semioval, attaining, as a rule, their greatest width near the antisicular end, which often appears truncated. Thecae in contact throughout, very closely arranged, numbering 16 to 20 in 10 mm; those near the sicula being directed outward and curved, the curvature gradually increasing toward the middle where they are strongly curved; becoming more ascending toward the antisicular end, where they are nearly straight and subparallel to the axis of the rhabdosome. Apertural margins regularly and deeply concave, mucronate extensions of the apertures long, narrow and in the compressed state of nearly uniform width, or sometimes appearing thickened or club-shaped at their distal ends, when more than the lateral margin of the extension is exposed. The character and length of the sicula has not been ascertained. A short stout sicular spine has been noticed in several specimens.

*Position and localities.* In the last layers of graptolite bed 2 (Tetragraptus horizon), and throughout the horizon with Didymograptus bifidus. Also in the next horizon with Diplograptus dentatus as well at the Deep kill, as at Mt Moreno. In Canada this form has been found, according to Hall and Lapworth, only in the St Anne beds, representing there the horizon with Didymograptus bifidus. Ami records it also from an outcrop near the city hall of Levis, in association with Didymograptus bifidus, etc. and from a locality on the Chaudière river. Gurley observed it also in suites of graptolites from the Beekmantown beds of Arkansas and Nevada. It is known from the Middle Skiddaw slates of the Lake district of England, where it is found associated with P. angustifolius; and from south Scotland.

Fig. 98 Phyllograptus anna Hall. Marginal portion of rhabdosome, to show the appearance of the thecal apertures in the compressed condition. Deep kill. x4.5

*Remarks.* This form is easily recognized, as pointed out by Hall and Elles, by its small size and the great number of thecae in a given unit of length. This is greater than in any other species and goes, in the Deep kill specimens, beyond the number obtained by the above cited authors. The greater width of the end is also, though not an unfailing, yet a striking character of the majority of the specimens, and the acute slender form of the mucros serves also to distinguish this species from the associated forms; specially from dwarfed specimens of P. ilicifolius, which have been noticed in the material.

Fig. 99 Phyllograptus anna Hall. Ashhill quarry at Mt Moreno. x5

The specimens observed in the last horizon of the Deep kill section have a still more condensed aspect, their thecae number as much as 22 in the space of 10 mm, and the total size attained is not more than 3.6 mm. They represent clearly a last dwarfed and paracmic mutation of the species, which might be designated as P. anna *mut.* ultimus [pl.15, fig.29, 30].

In the beds with Diplograptus dentatus exposed at Mt Moreno a form of P. anna is extremely common, which, while, by its outline,

close arrangement and direction of thecae, still falling within the boundaries of the original description of that species, differs distinctly by the absence of the long apertural mucros and generally less compact or truncate shape. Its outline is uniformly oval, with the broader part forming the sicular end [pl.15, fig.28, and text fig.99], and it is always small, none of the specimens surpassing 6 mm in length. This mutation I propose to designate as P. anna *mut.* pygmaeus. It is however possible that this is a last and pygmaean mutation of P. ilicifolius.

Several specimens of this species distinctly show a fine chitinous thread passing longitudinally through the rhabdosome, which has the appearance of being the nema of the sicula, incorporated into the rhabdosome.

### Genus *incertae sedis*

#### STROPHOGRAPTUS gen. nov.

Etymology: *strophos*, bent; *grapho*, I write.

*Description.* Bundles of long, thin, flexuous, carbonaceous, subparallel fibers which do not bifurcate. Thecae not projecting from branch or rhabdosome (?), thecal apertures appressed in one row. Virgula not observed. Apertures connected by median depressions (perhaps of secondary origin and indicating the position of the coenosarc).

*Remarks.* The type species of this genus, Strophograptus trichomanes, occurs in numerous bundles of fibers on the slabs of graptolite bed 6, zone with Diplograptus dentatus. Bundles of finer and unbranching fibers are also found on slabs of the preceding zones. As these masses are intermixed with the typical graptolites, consist of the same carbonaceous matter and exhibit regularly distributed thecal apertures, but can not be referred to any of the graptolite genera with which they are found associated, they must be recognized as representing a separate generic type.

Emmons established a genus, Nemagrapsus [1855, 2:109], for threadlike, chitinous bodies, and described two species, viz N. elegans and N. capillaris. The first was recognized by Hall as being based on a

fragment of his Coenograptus gracilis, and the second species has then been considered as the genotype of Nemagraptus. This genus has had a somewhat checkered career; at first it was not recognized by some, as Hall, but later its right of existence was asserted by Lapworth and Gurley. Dr Gurley collected identical material in the same horizon as Emmons (Normanskill shale, cited by Emmons as Taconic slates of Columbia county). From this genus, as based on Nemagrapsus capillaris, in which Emmons was unable to find apertures, the present one is distinguished by its lack of branching[1]. Gurley has erected still another genus, Phycograptus, for similar threadlike bodies, which also have been frequently observed by the writer in the Normanskill shales. This genus, to which two species are referred, is likewise represented by unbranching, long, carbonaceous fibers with a central row of pits or apertures, but the fibers are distinctly segmented by partitions midway between the pits and possess marginal grooves. The writer has obtained a specimen of Phycograptus at Mt Moreno, to be more fully described and figured later on, which shows a short cylindric axis, from which the innumerable Phycograptus fibers proceed in verticillate arrangement. Whether the fibers of Strophograptus are similarly connected with a stem is not known as yet; but their regular subparallel arrangement in bundles would indicate that the component fibers of these bundles belong together.

### Strophograptus trichomanes sp. nov.

Plate 4, figures 17–20

*Description.* Bundles of thin, flexuous fibers (branches?), the fibers attaining a length of 13 cm and a width of .2 mm. Thecal apertures circular to transversally oval pits on slight prominences, numbering about 8 in 10 mm; fibers contracted between the pits by one fourth or one third of their width.

[1] Elles and Wood have meanwhile, in the third part of the *Monograph of the British Graptolites* very properly replaced Hall's term Coenograptus, which though younger has been generally accepted, by Emmons's term Nemagraptus which has the right of priority.

*Position and locality.* Zone with Diplograptus dentatus at the Deep kill.

*Remarks.* Similar strands of long, fine threads occur also in the two subjacent horizons. They belong to another species, as suggested by the smaller width of the fibers, if they are at all congeneric with this fossil, for no thecal apertures have as yet been discerned on them.

## Suborder B GRAPTOLOIDEA AXONOPHORA Frech

## Family DIPLOGRAPTIDAE Lapworth

### DIPLOGRAPTUS McCoy. 1854

The genus Diplograptus makes its first appearance in the uppermost of the graptolite beds of the Deep kill (graptolite bed 6, horizon with D. dentatus) and does not attain the acme of its development till the Trenton period. We shall, for this reason, reserve the more detailed characterization and discussion of this genus for the next memoir, which will contain the descriptions of the graptolites of Trenton and later age, and mention here provisionally only a few of the most important facts.

The genus was originally proposed by McCoy in place of Barrande's Diprion, a name which was preoccupied. Like Barrande's term, it was intended to include all forms with two series of thecae. By the separation of several groups of biserrate forms as genera, as Climacograptus and Glossograptus, the genus has been restricted to diprionid forms with a straight virgula, inclined thecae and normal, mucronate or nonmucronate apertures. The various forms comprised by this definition have since been subdivided by Lapworth [1873], and Frech has proposed [1897] a division into two groups according to the presence or absence of apertural spines.

The four species described here, viz D. dentatus, longicaudatus, laxus and inutilis, are evidently to be referred to Diplograptus proper.

It has been demonstrated by the present writer that the rhabdosomes of Diplograptus are parts of a person of a higher order (synrhabdosome), they

being united in the center by a funicle and a central disk [p.528], and that from the latter originate the gonangia in which new siculae are produced; and Wiman has shown that the apparent biserial arrangement of the thecae is produced by one series, the thecae budding alternately on opposite sides [p.538].

### **Diplograptus dentatus** Brongniart sp.

Plate 17, figures 10-13

Fucoides dentatus Brongniart. Hist. Végét. Foss. 1828. 1:70ff, pl.6, fig.9–12

Graptolithus pristiniformis Hall. Geol. Sur. Can. Rep't. 1857. p.133

Diplograptus pristiniformis Hall. Geol. Sur. Can. decade 2. 1865. p.110ff, pl.13, fig.15–17

Diplograptus pristiniformis Nicholson. Quar. Jour. Geol. Soc. 1868. 24:140, pl.5, fig.14, 15

Diplograptus dentatus Hopkinson & Lapworth. *Ibid.* 1875. 31:656ff, pl.34, fig.5a–k

Diplograptus dentatus Ami. Geol. Sur. Can. Rep't, ser.2. 1889. v.3, pt 2, p.117k

Diplograptus dentatus Gurley. Jour. Geol. 1896. 4: 298

Diplograptus dentatus Elles. Quar. Jour. Geol. Soc. 1898. 54:517ff

Diplograptus dentatus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p. 570

This type, which is very common in the graptolite beds at the dam in the Deep kill section and at Mt Moreno, not only presents a great variety of appearances, some of which are represented by the camera tracings but also considerable variations in its dimensions.

*Description.* The rhabdosomes are as a rule narrow, attaining their full width (1.8 to 2.1 mm) at an early stage of their growth, and maintaining this throughout. Perfect specimens attaining a length of 45 mm have been observed, but fragments indicate that they grew still beyond that size. The thecae are closely arranged; they number 10 in 10 mm in most specimens, but in the earliest parts of a few number 14 to 16 and in the later portions of

the rhabdosome as much as 12. In normal specimens they appear as subacute denticulations, are narrow, forming an angle with the axis not greater than 20°, are free for one third of their length, and possess a slightly concave outer margin, slightly mucronate or acute apertural extension, straight or slightly concave apertural margin, which forms an angle of 80° to 90° with the axis. There are however other specimens in which the outer margins are strongly rounded, the apertural margin is straight or slightly convex, and some in which the thecae appear to be free for at least one half or even two thirds of their length.

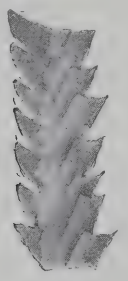

Fig. 100 Diplograptus dentatus Brongniart *sp.* Fragment of middle portion of rhabdosome. Shows two aspects of thecae. Ashhill quarry at Mt Moreno. x5

The virgula which is often seen to extend through the rhabdosome is straight and distinct, but apparently not so strong as indicated by Hall's figure. A strong median sicular spine, about 5 mm long, has been observed in several specimens, as well as two short lateral spinules.

*Position and localities.* This is the most characteristic and common graptolite of the last horizon in the Deep kill section and is there restricted to the same. It occurs with equal frequency in the somewhat older bed at Mt Moreno, near Hudson. In Canada it is found in the homotaxial Point Levis zone. Gurley records it from Arkansas. In the Upper Skiddaw slates (Ellergill beds) it has been observed in many localities. Hopkinson and Lapworth report it also from the Upper Arenig of Ramsey island and the Llanvirn quarry in Wales. In Sweden it has been found at the top of the Phyllograptus zone (subzone with Phyllograptus cf. typus).

*Remarks.* The great variety of appearances as well as of dimensions of this species has been commented on by Hopkinson and Lapworth, and Elles. It is also very noticeable in the Deep kill material and still more so in that from the Mt Moreno, which contains numerous specimens that attain a width of 2.6 mm—thus surpassing considerably the maximal width observed by Miss Elles—and have not more than nine thecae in the space of 10 mm. These specimens differ so materially from the originals of

Hall's description that they would have to be separated if they were not intermixed with numerous transitional and some typical forms. It is however unmistakable that here a strong tendency to the production of a coarser form is displayed.

### Diplograptus inutilis Hall

Plate 16, figures 12, 13

Diplograptus inutilis Hall. Geol. Sur. Can. decade 2. 1865. p.111, pl.13, fig.14

Diplograptus inutilis Gurley. Jour. Geol. 1896. 4:298

Diplograptus inutilis Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.570

A few specimens of a diprionid form agree with the incomplete original description and figures of this not very well known species.

*Description.* The rhabdosome was probably of moderate size (length of one specimen 7 mm, of the fragment of another 11.4 mm); attaining a maximal width of 2.4 mm, from which it gradually tapered to the antisicular end. The thecae are curved; number 12 to 10 mm; are inclined about 40°; in contact for one half of their length. Their outer margins are strongly curved, first convex, then concave, abruptly bending outward near the apertures and forming a blunt mucronate extension of the aperture, which extends at right angle to the axis. The aperture is straight or slightly convex and also approximately perpendicular to the axis. Virgula very strong. Appendages of sicular end not observed.

*Position and locality.* Very rare at the Deep kill in the horizon with Diplograptus dentatus, to which it is also restricted in Canada [Hall and Gurley].

*Remarks.* The specimens here figured agree with Hall's originals in the width of the rhabdosome, the perpendicular position of the free portions of the thecae in regard to the axis, the number of thecae in a given space and the mucronate prolongations of the apertures. The type specimens were also found in the same association, in the Quebec shales of Point Levis, as those here described.

### Diplograptus laxus sp. nov.

Plate 16, figures 1–10

Diplograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.571

A small species of Diplograptus, presenting some very peculiar characters, occurs frequently in bed 7 (zone with D. dentatus) of the Deep kill section and in beds of the same horizon at Mt Moreno.

*Description.* Primary disk not observed. Nema short, attaining a length of 9 mm or more, relatively stout, and expanded into a cucumber-shaped vesicle [pl.16, fig.3]. Rhabdosome small (maximal length observed 13.4 mm, prevailing length only about 10 mm) and narrow, as a rule not wider than 1 mm, of nearly uniform width. Sicular end provided with two short, curved lateral and a short median spine (the former, apertural spines of first thecae, the latter, probably median spine of sicula). Thecae numbering 10 to 12 in 10 mm, curved, the angle of inclination increasing from 10° in the basal to 30° in the apertural portion of the thecae; overlapping but one fourth of their length; their outer margin concave, first subparallel to the axis of the rhabdosome and then turning rather abruptly outward. The apertural margin slightly convex and oblique to the general direction of the thecae, forming a short, blunt apertural denticle in the compressed material.

*Position and localities.* Frequent on the surface of graptolite bed 7 (belonging to the zone with D. dentatus) of the Deep kill section and in similar association at Mt Moreno near Hudson.

*Remarks.* I am not aware of any form from which this species could not be readily distinguished either by its small size or the peculiar shape of its thecae. The similarly minute D. putillus Hall, which occurs in the Upper Champlainic shales, has its thecae much less inclined and becoming in their distal portions subparallel to the rhabdosome instead of increasing in divergence as the thecae of this species do. The same difference exists between this species and the equally old, small European form,

D. teretiusculus Hisinger sp. Frech describes [1897, p.628] a form from a north German glacial boulder with thecae projecting "swallow-nest-like" as D. sertularioideus. With that species our specimens, specially those which were apparently slightly macerated before becoming buried [pl.16, fig.8], possess some similarity in the shape of the thecae. The consideration of a possible identity of the two species is however precluded by the slenderness of the rhabdosome of our form when compared with the broader and more compact shape of the European species.

A feature worth special mention is the apparently vesicular expansion of the nema. This has hitherto not been observed in any American species of Diplograptus, though it is known to European paleontologists from D. vesiculosus Nich. and D. appendiculatus (Törnq. ms) em. Elles.

### **Diplograptus longicaudatus** sp. nov.

Plate 16, figure 11

*Description.* Rhabdosome small, attaining its full width (2.8 mm) near the sicular end. The thecae are closely arranged (16 in 10 mm); inclined at an angle of 35° to 40°; in contact for about half their length; their outer margins strongly concave; the apertural margins strongly convex; the blunt marginal angles turned downward. Virgula stout and long. Sicula not observed.

*Position and locality.* Extremely rare in the horizon with Diplograptus dentatus at the Deep kill.

*Remarks.* This species is based on a single specimen. This could in some of its features, be called an extreme form of D. dentatus, notably in the possession of the long sicular, terminally filiform spine (virgella) and the close arrangement of the thecae. It differs, however, too much from that species in the character and inclination of its thecae to be safely identified with it.

### GLOSSOGRAPTUS Emmons. 1856

The author of the genus saw its distinctive characters in the ligulate outline and rounded extremities, as its name implies, but not in the presence of the long spines, for he described in the same paper an equally spinous form under Diplograptus. Hall [1865, p.43] did not recognize the genus, as, in his opinion it is based on a species of Diplograptus with ciliate appendages on the cell margins, "and no characters are given to show its generic distinction"; and Frech [1897, p.631] concurs with Hall in this view, stating that, as these appendages show all gradations in the diprionid graptolites and in Pristiograptus, they are not suited for generic distinctions. On the other hand, the same author divides the species of the genus Diplograptus into two sections, one without and one with thecal spines, considering the latter section as coinciding with the genus Glossograptus, as defined by Lapworth. The latter author [1873, p.504], however, has proposed to restrict the term to forms in which, as in Emmons's type, not only is each theca furnished with two long spines or fibers, extending outward from the angles of the aperture, but the polypary itself is ornamented in addition with two opposite longitudinal rows of gigantic isolated spurs, developed along the median line of the periderm at right angles with the thecae. Elles [1898, p.521ff] unites under Glossograptus all diprionid species with long thecal spines, which indeed seem to form a small characteristic group. We give the genus here the same compass.

#### Glossograptus hystrix sp. nov.

Plate 16, figures 27–29

Glossograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.571

*Description.* Sicula, nema and primary disk not observed. Rhabdosome small (4.5 mm length of largest specimen observed), relatively wide (about 1.6 mm), with subparallel margins. Thecae closely arranged, numbering 20 in 10 mm, inclined at the low angle of about 25°, overlapping three fourths of their length, exhibiting straight outer margins and straight

apertural margins, which are approximately perpendicular to the axis. Entire rhabdosome bristling with straight, long (1.4 mm) spines, four of which are placed at the sicular end and directed parallel to the axis, while those in the middle of the rhabdosome have a horizontal position and those found near the antisicular end are directed upward. Each theca is provided with at least two spines, which are situated on either side of the aperture, and apparently also with others on the lateral faces or the outer margin of the thecae.

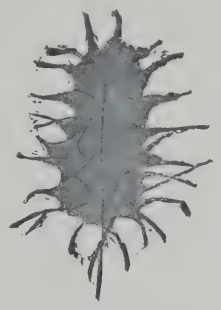

Fig. 101 Glossograptus hystrix sp. nov. Rhabdosome. Deep kill. x8

*Position and localities.* This form is rare (only four specimens having been found) in the shale at the dam, belonging to the horizon with Diplograptus dentatus and Climacograptus? antennarius; and in beds at Mt Moreno, containing forms of an early phase of this horizon.

*Remarks.* From the homotaxial horizon in the Ellergill beds in England not less than three species have become known, viz G. fimbriatus, hincksii and armatus. With the last of these, the form here described possesses the most similarity, both agreeing in the dimensions and shape of the rhabdosome; the Ellergill form, however, has fewer and longer spines, which are reflexed.

### **Glossograptus echinatus** sp. nov.

Plate 16, figures 30-32

*Description.* Primary disk, nema and sicula not observed. Rhabdosome of medium size, a perfect specimen measuring 19.5 mm, wider in the middle than at the ends, about 1.2 mm wide at the sicular end, 3 mm in the middle (excluding the spines) and 2.2 at the antisicular end. Thecae, narrow tubes numbering 12 in 10 mm, inclined at 15°, three times as long as wide, in contact about one half of their length; their outer margins concave; their apertural margins straight, passing obliquely to the axis of the thecae; their outer margins protracted into stout spines (1.5 mm long), which are approximately perpendicular to the axis of the rhabdosome. The sicular

end of the latter provided with two longer outer and two shorter inner spines.

*Position and locality.* Very rare in the horizon with Diplograptus dentatus at the Deep kill.

*Remarks.* This species appears to be a vicarious form of the British G. fimbriatus of the same horizon, similarly as G. hystrix resembles G. armatus, another species of the British Ellergill beds. Our type possesses a shape of the rhabdosome, thecae and spines, much like G. fimbriatus, but is larger, broader and has larger and less closely arranged thecae. The spines are also, judging from the drawings of the British form, stouter in our species. In the character of the spines the present species would seem to approach G. hincksii, from which it differs however in the relative distance of these spines, which are more closely set in the Deep kill form (one to each theca, while in G. hincksii, according to Elles, probably only every second or third theca possessed spines).

Fig. 102 Glossograptus echinatus sp. nov. Thecae. Deep kill. x6

TRIGONOGRAPTUS Nicholson. 1869

Nicholson proposed this genus [1869, p.231] for a form, which was discovered by him in the upper Skiddaw slates and cited the following as its principal characters: "Frond simple, diprionidian, rapidly tapering toward the base and having perfectly plain lateral margins without denticles. Cell partitions alternating with one another, and springing from an undulating or zigzag solid axis. A common canal is probably present, in which case the axis must be excentric; but the evidence on this point is incomplete."

Of the features noted here, only the perfectly plain margins without denticles remain as a distinguishing character from the other Diplograptidae; for the frond is rapidly tapering only in the type species, T. lanceolatus, but not in the species here described, which has also been referred by Nicholson to his new genus; the cell partitions alternate in all Diplo-

graptidae on account of their origin by alternate budding; and the axis was originally described as having a zigzag form in T. lanceolatus, while that of T. ensiformis has always been known to be straight or but slightly undulating [pl.17, fig.4]. Nicholson's observation of a zigzag axis in the type species appears not to be verified by Elles, who, after inspection of that author's type material, cites the greater inclination of the thecae in T. lanceolatus as the only difference between the two species of the genus.

Thus the indentate margin remains the only distinctive character of the genus. This straight, undivided margin is due to a peculiar obliquity of the apertures to the axis of the thecae, as some of our specimens clearly show [fig.9], the apertural angles of the thecae being approximately equal to their inclination angles, both forming thus alternating angles between parallels.

The oblique position of the apertures is also the only difference I am aware of, between this genus and Diplograptus; the former should, hence, probably be regarded as representing an aberrant branch of the Diplograptidae, one of the variety of forms which are characteristic of the first outburst of that family, and which soon disappear again. Trigonograptus can not be considered a climacograptid, though where, by maceration or compression, the thecae have slightly separated, the appearance of a climacograptid is sometimes produced.

### Trigonograptus ensiformis Hall sp.

Plate 17, figures 1-9

Retiolites ensiformis Hall. Geol. Sur. Can. decade 2. 1865. p.114ff, pl.14, fig.1–5

Trigonograptus ensiformis Hopkinson & Lapworth. Quar. Jour. Geol. Soc. 1875. 31:659ff, pl 34, fig.8a-c

Trigonograptus ensiformis Ami. Geol. Sur. Can. Rep't, ser. 2. 1889. v.3, pt 2, p.117k

Trigonograptus ensiformis Nicholson. Geol. Mag. ser. 3. 1890. 7:340, 341, fig.1, 2

Trigonograptus ensiformis Gurley. Jour. Geol. 1896. 4:299

Trigonograptus ensiformis Elles. Quar. Jour. Geol. Soc. 1898. 54:523, 524, fig.34

Trigonograptus ensiformis Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.571

There occur in great number on the shales at the dam in the Deep kill section gigantic lanceolate rhabdosomes, mostly without apparent trace of structure, which, as their characteristic outline and size readily suggest, belong to Hall's Quebec species, Trigonograptus ensiformis.

*Description.* Rhabdosome long, lanceolate, reaching its maximum width (7 mm or more) about 20 mm from the sicular end and converging in a like degree at the antisicular end. The sicular end provided with a slightly geniculate, bluntly terminating, short appendage; antisicular virgular extension or nema not observed. Total length unknown; fragments [fig.3] attaining a length of 80 mm and more, so that the rhabdosome may have reached a size of 1 dcm. Margins in most specimens perfectly linear and unbroken. Thecae indicated by the thick interthecal walls; alternating, in contact throughout their whole length, numbering 10 to 11 in the sicular portion and, mostly, only 8 within the space of 10 mm in the mature portions. The apertures, which are rarely well shown [fig.7, 9], are subquadratic, lying in one line and obliquely to the axis of the thecae; they are without any apertural appendages. The thecae form an angle of about 45° with the axis of the rhabdosome. Along the latter, in somewhat macerated specimens a perfectly straight, stout virgula is seen to pass. The test does not show any traces of reticulation, but is smooth and thick, and often bordered by longitudinal thickened lines, apparently formed by the confluence of the lateral apertural margins.

*Position and localities.* In graptolite bed 6 of the Deep kill section, belonging to the zone with Diplograptus dentatus. The species has been also observed, though less frequently and in smaller specimens, in the base of this horizon at Mt Moreno.

Hall's types came from the Quebec group at Point Levis. According to Gurley, it occurs there in the upper zone, with Diplograptus

dentatus. The same author cites it in his list from Arkansas. Hopkinson and Lapworth identified a small, more obtusely pointed form, which they obtained from the Lower Arenig of Ramsey island in Wales, with this species. The latter, if not identical, represents a closely related smaller type. Typical specimens were collected and described by H. A. Nicholson from the Upper Skiddaw slates (Ellergill beds) which are homotaxial with the beds with Diplograptus dentatus in the Point Levis and Deep kill regions. Miss Elles also had typical material from the same horizon of the Skiddaw slates for investigation.

*Remarks.* This species was doubtfully referred by its author to Retiolites. When Nicholson erected the genus Trigonograptus, he assigned Retiolites ensiformis to it, though the genotype was described as having a zigzag virgula, and this form has a straight one.

It appears that neither in Canada nor in England specimens of such gigantic size were observed as the fragments in the Deep kill beds must have come from. Hall's largest specimen measured nearly 2½ in. (about 62 mm), while Miss Elles had a fragment measuring 38 mm. The one reproduced here in figure 3 measures 80 mm.

## Family CLIMACOGRAPTIDAE Frech

### CLIMACOGRAPTUS Hall. 1865

This genus, which becomes so prominent, both in number of species and individuals, in the higher zones of the Lower Siluric, is represented by but two species, one of which, C. pungens, though an undoubted Climacograptus, is a very diminutive form, while the other, C. ? antennarius, can be referred only with doubt to climacograptus.

On account of this meager representation of the genus in the lower Lower Siluric, we reserve the discussion of its characters for the next memoir, in which we shall be better enabled to illustrate them with the aid of the larger and more typical Trenton material.

### Climacograptus pungens sp. nov.

Plate 16, figures 14-20

Climacograptus sp. nov. Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.571

The finding of two small rhabdosomes, in the Deep kill shale with Diplograptus dentatus, has proved the appearance of the genus Climacograptus at this early date in this region. Later on, numerous specimens of the form here described were found in a still somewhat older subhorizon at Mt Moreno, near Hudson. As the only other species known to occur so early, viz C. scharenbergi Lapworth [Ellergill beds of England; *see* Elles, 1898, p.519], is a distinctly different form, and the fragments can not be readily assigned to any younger species, they are here described as representing a new species.

*Description.* Rhabdosome small (length of largest specimen 18 mm, but average length only 12 mm) and narrow (1.6 in one case, as a rule not over 1.3 mm wide), of uniform width. Sicular end provided with two very long (12 mm or more), extremely slender and flexuous appendages. The thecae are short, closely arranged, numbering 10 to 12 in 10 mm; the apertures relatively large, broadly oval, provided at their outer margin with a short spine [pl.16, fig.14]. The sutural groove is little distinct, slightly undulating. The nemacaulus relatively stout and long.

*Position and localities.* Rare in the horizon with Diplograptus dentatus at the Deep kill; common in the same horizon at Mt Moreno.

*Remarks.* From C. scharenbergi this form is readily distinguished by the character of the sutural groove, which in that species is deep and characteristically deflected from side to side, horizontal grooves setting out from the outer points of each angulation. The long appendages and the apertural spines are also a feature not observed in that species, which besides, has a greater number of thecae within a space of 10 mm.

## Climacograptus? antennarius Hall (sp.)

Plate 16, figures 21–26

Climacograptus antennarius Hall. Geol. Sur. Can. decade 2. 1865. p.112, pl.13, fig.11–13

Diplograpsus antennarius Nicholson. Quar. Jour. Geol. Soc. 1868. 24:139

Cryptograptus? antennarius Lapworth. Ann. and Mag. Nat. Hist. ser 5. 1880. 5:174

Cryptograptus antennarius Gurley. Jour. Geol. 1896. 4:299

Cryptograptus? antennarius Elles. Quar. Jour. Geol. Soc. 1898. 54:519ff, fig.31

Climacograptus antennarius Roemer & Frech. Lethaea palaeozoica. 1897. 1:611

Cryptograptus antennarius Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.571

*Description.* Rhabdosome medium sized (about 20 mm), of nearly uniform width (2.7 to 3.5 mm); provided with a stout sicular spine and two long, slightly curved, rigid lateral spines, diverging at an angle of 100° to 110° and attaining a length of about 5 mm. Sicula not distinctly observed. Thecae closely arranged (9 to 11 in 10 mm); parallel to the axis of the rhabdosome; apertures transverse oval incisions. Nemacaulus stout and straight, its proximal extension relatively very long, measuring 18 mm in one instance.

*Position and localities.* Common in the horizon with Diplograptus dentatus, exposed at the dam of the Deep kill. Hall's types came from the Quebec group at Point Levis (upper horizon). Nicholson and Elles have recognized this form among the Skiddaw graptolites, and record it as occurring at various places in the Upper Skiddaw slates; Gurley lists it also among the Arkansas graptolites.

*Remarks.* The synonymy shows that this small form, which by its outline and distal spines appears so well characterized, presents indeed, considerable difficulties to a determination of its generic relations. While Hall described it as a Climacograptus, it has subsequently been referred to Diplograptus by Nicholson, to Cryptograptus by Lapworth, Gurley and

Elles, and again to Climacograptus by Frech, who does not recognize the genus Cryptograptus. An inspection of the numerous specimens from the Deep kill explains this uncertainty; for, while the outlines of the rhabdosomes are sharply defined, they are nearly always uninterrupted and straight, and the surfaces of the rhabdosomes are perfectly smooth. The apertures of but one specimen [fig.22] could be seen fairly well in the frontal aspect, and the thecae of another in their profile view [fig.24]. From these observations I infer that the thecae had the same position as in Climacograptus. Moreover, the strong development of the distal spines is a character most developed in the later species of Climacograptus, and, hence, to some extent indicative of this genus. Yet, in its habit this form is by no means a typical Climacograptus, and for this reason it is here referred with doubt to that genus.

Lapworth expressed his belief that this species may belong to his genus Cryptograptus; and the general form of the rhabdosome and the three strong distal spines are characters certainly very similar to those of the genotype Cryptograptus tricornis; but the thecae of that form are described and figured as inclined, and so are those of Cryptograptus hopkinsoni, which, in the profile view, remind one strongly of those of Diplograptus dentatus.

The perpendicularly projecting spinules, observable according to Hall along the margins of the rhabdosomes in some specimens, have not been noticed in the Deep kill material.

### RETIOGRAPTUS Hall. 1865

Hall separated the genus Retiograptus from Barrande's genus Retiolites, making the species described here the type of the new genus and stating that the three species which he refers to it "are nearly related to Retiolites; but the texture of the specimens examined, and the arrangement of the parts, differ so much from authentic specimens of Retiolites geinitzianus, that I have separated them under the above designation." The author of Retiograptus concedes that the three species united under this generic designation present some important points of difference,

one from the other. In fact, the two other forms appear to represent structures entirely different from that of R. tentaculatus. No forms fitting into the generic diagnosis of Retiograptus have been found elsewhere. The genus has, however, been emended by Frech [1897, p.607], who, asserting the similarity of its rhabdosomes with those of Gothograptus and Retiolites, sees the diagnostic characters of the genus in the lesser development of the reticulate structure, which he infers is only suggested by a row of hexagonal meshes along the margin, in the rectangular arrangement of the thecae, the presence of spines and the resistibility of the virgula. From the aspect of some specimens of R. tentaculatus [pl.16, fig.35] it is to be inferred that the entire periderm was reticulate in one of its layers at least, and that the marginal meshes correspond to apertural thickenings such as are also found in Retiolites. This would leave as distinguishing characters between the two genera only the rectangular arrangement of the thecae and the presence of short apertural spines.

If the thecae were placed perpendicular and the apertures straight and parallel to the axis of the rhabdosome, the genus, as represented by the genotype here described would not be referable as a reticulate branch to Climacograptus, where the thecae hold positions parallel to that axis and the apertures form more or less transverse notches in the straight margin; but it should, in the writer's opinion, be considered to represent an extreme form of Diplograptus, where the angle of thecal inclination has become 90°, approaches to which are found in some other species of that genus and also in some of Retiolites, as e. g. R. venosus from the American Clinton beds.

### **Retiograptus tentaculatus** Hall

Plate 16, figures 33-35

Graptolithus tentaculatus Hall. Geol. Sur. Can. Rep't for 1857. p.134

Reteograptus tentaculatus Hall. Geol. Sur. Can. decade 2. 1865. p.116f, pl.14, fig.6–8

Retiograptus tentaculatus Matthew. Roy. Soc. Can. Proc. and Trans. 1894. 11:114

Reteograptus tentaculatus Gurley. Jour. Geol. 1896. 4:299

Reteograptus tentaculatus Roemer & Frech. Lethaea palaeozoica. 1897. Bd 1, p.608

Retiograptus tentaculatus Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.571

*Description.* Rhabdosome small (maximal length about 20 mm), elongate elliptic, gradually and slightly widening toward the middle, where it attains a width of about 4 mm, and equally narrowing toward the antisicular end. Periderm finely reticulate, the meshes subcircular to subhexagonal. Sicular end provided with two shorter straight and two longer curved lateral spines, which assume a direction subparallel to the axis of the rhabdosome. Thecae placed rectangularly to the virgula, numbering 10 to 14 in 10 mm, each provided with a stout, straight or slightly downward curved spine and a ringlike thickening of the apertural margin. Apertures straight, parallel to the axis of the rhabdosome.

*Position and localities.* In the shale exposed at the dam in the Deep kill section, belonging to the zone with Diplograptus dentatus and in the somewhat older beds at Mt Moreno near Hudson. Hall's material came from the same horizon at Point Levis. Matthew referred a form from the division 3 d of the St John group with doubt to this species. As all the other species of 3 d are those of the Tetragraptus zone, it is not likely that R. tentaculatus is present in that horizon.

*Remarks.* Some of the specimens of this species possess a considerable similarity with Glossograptus fimbriatus Hopkinson, which occurs in the homotaxial Ellergill beds of the Upper Skiddaw slates; they differ still in the smaller length of the spines and smaller number of thecae within a certain space.

In one specimen [fig.35], which is well preserved and which exhibits a distinct reticulation, some of the apertural spines are prolonged into chitinous filaments, which, bending downward, unite with those of the next preceding thecae in a manner suggesting the marginal structure of Lasiograptus. The latter structure according to Törnquist [1890, t.2, fig.27] and Frech [1897, p.672], consists of the distal, coarsely perforated portions of the thecae.

## ADDENDUM

### CARYOCARIS Salter and DAWSONIA Nicholson

Associated with the graptolites of the Deep kill and Normanskill beds, we have found numerous small variously shaped bodies which consist of a substance that is similar to, but as a rule, more tenuous than that of the graptolites. For one group of these bodies the generic term, Caryocaris, has been proposed by Salter [1863, p.139], for another that of Dawsonia by Nicholson [1873, p.139]. The former were considered crustaceans, the latter "ovarian capsules" ("grapto-gonophores") of graptolites. Gurley [1896, p.85ff] has maintained that both are graptolites. As, at least, in regard to one group, the Dawsonias, our material tends to verify his observations, we have appended here the descriptions of the representatives of both groups occurring in the lower graptolite beds; but wish it understood that we consider their taxonomic position not yet determined.

The substance and texture of the test of all these forms is one of their characteristic features by which they can be readily recognized. It is apparently of a chitinous nature, but mostly thinner than that of the graptolites, of less luster, possessing often a light purplish tint, also observed by Etheridge, Woodward and Jones[1] in regard to Caryocaris wrightii, and above all an extremely delicate, irregular corrugation or wrinkling, the wrinkles often assuming the appearance of scales or regularly overlapping tiles [pl.17, fig.17]. This corrugation, which is never found so strongly developed on the periderm of the graptolites, is an indication of the thinness and flaccidity of the test of the forms under discussion. It often appears like a shriveling, but is in most cases clearly superinduced by the incipient and minute cleavage or slipping of the rock. Its character is indicated on the figures, which also show that the wrinkles cross the specimens in no definite direction, but that the latter depends entirely on the accidental position of the specimens to the cleavage planes in the rock.

[1] Rep't of the Committee on the Fossil Phyllopoda of the Palaeozoic Rocks. 1883, p.7.

The carbonaceous film which we find in the shale is probably but a residuum of a somewhat thicker and more composite test; for we observe that the numerous shells of linguloid and oboloid brachiopods in the same shales are in exactly the same tenuous condition. The latter are, however, known to have lost their phosphate of lime component. As further, Salter reports that the tests of Caryocaris wrightii are often quite solid for their size and appear to have had a good deal of lime in their composition, it is possible that all these now very tenuous shells are leached out to a considerable degree.

### CARYOCARIS Salter. 1863

The genus Caryocaris was proposed by Salter for small chitinous bodies occurring abundantly in the Skiddaw slates and described by him as follows:

> A long, pod-shaped, bivalved carapace (with distinct hinge pits), rounded anteriorly, subtruncate behind, and with the back and front subparallel. The surface is smooth, or with only oblique wrinkles near the margins, but with no parallel lines of sculpture. Body?, telson and appendages?
>
> All I know of this pretty little Crustacean, an inch long, and rather more than one third of an inch wide, is contained in the above note.

Only one species, C. wrightii, was described. In a restoration of the same the presence of a short abdomen, with a lanceolate telson and stylet was suggested. Dr Hicks, in 1876 [Quar. Jour. Geol. Soc. 32:138], added the description of another species from the Cambric of Wales. Etheridge, Woodward and Jones have, in the paper cited above, described the genus as one of phyllopod crustaceans of the Palaeozoicum and added that, while they have not observed the abdomen, as restored by Salter, Mr Marr has found, in association with Caryocaris, "some small, slender spines or pointed styles . . . which do not contradict Salter's ideal figure." They also state that the ventral and anterior margins are thickened with a raised rim, while the dorsal margin has no rim, as it has in Salter's figure. The "hinge pits" cited by Salter could not be found by these authors.

Dr Gurley noticed in the collection from the Beekmantown shales of Point Levis, Canada, and the Upper Beekmantown of Summit in Nevada, small, winged bodies in great number, which he referred to this genus, arranging them in three specific groups. One of these he considered identical with the genotype, C. wrightii. Gurley holds now that what hitherto has been described as Caryocaris are only appendages, and that the complete body [text fig.103] consists of "two symmetrically paired lateral appendages attached to the distal end of a single median proximal portion on which [he believed] thecae could perhaps be traced." It is stated at the end of the generic description that "it is needless to add (as Lapworth points out) that it is not, as Salter supposed, a crustacean, but from its resemblance to Dawsonia appears to be a graptolite."[12]

Fig. 103 Caryocaris wrightii Salter. From the Upper Beekmantown of Nevada. x2 (Copy from Gurley)

Our Deep kill specimens of Caryocaris [pl.17] fail to show either the more complicated structure, observed by Gurley, or anything suggesting thecae, but appear as nothing but pyriform bodies truncate at one end and bluntly acute at the other. One margin of one of the figured specimens [fig.17] has a distinctly raised rim on one side which gives the impression of being the result of a fracture through a part of the test, folded on itself. Our largest and best preserved specimen is 7.2 mm long and 2.8 mm wide. It has, hence,

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[1] We have not been able to find where Lapworth has expressed this view, but noticed that in 1876 [Catalogue of Western Scottish Fossils, p 7] Dawsonia is still cited among the crustaceans by this eminent authority on graptolites.

[2] Jones and Woodward have figured in their *Monograph of the British Phyllopods* a specimen of C. wrightii [pt 2, 1892, p.91, fig.6] which they had received from Prof. C. Malaise and which appears to retain a trifid tail partly extruded below the narrow extremity. They conclude on this evidence that, in this crustacean, style and stylets were all three dagger-shaped. It is obvious that the views of the British authors and of Gurley are greatly at variance; and our material consisting only of the podlike bodies does not permit us to select between the conflicting opinions. We suspect, however, that the supposed caudal appendage of Caryocaris and the trifid bodies here assigned to Dawsonia monodon Gurley are identical.

about the same dimensions as the lateral appendages of the forms referred by Gurley to C. wrightii, and is considerably smaller than the pod-like bodies described under this name from the Skiddaw slates. In outline and the position of the raised rim it agrees best with the appendages described by Gurley as C. curvilineatus from the Beekmantown at Point Levis, and the Upper Beekmantown of Nevada. We refer it therefore with some doubt to the latter species.

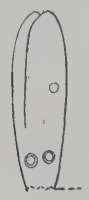


Fig. 104 Caryocaris oblongus Gurley. Showing conjoined lateral appendages. From the Beekmantown shales at Point Levis, Canada. x2 (Copy from Gurley)

In the United States National Museum there is a small suite of slabs, collected by C. D. Walcott in 1890, on the Mettanee river, ¼ mile above the North Granville bridge, in Washington county, N. Y. These slabs are covered with rather faint, structureless, carbonaceous films, which, in outline and size, are somewhat varying and indeterminate, but in general resemble flattened or burst apple seeds. In one or two places two of these films are united in such a fashion as to suggest that they originally belonged together [pl.17, fig.16]. On a label written by Dr Gurley, one of the latter specimens is sketched, and this is added, "resembles C. oblongus most, but more rounded oval." The material in hand does not allow any definite identification or description and we have been unable to secure better specimens at the original locality.

### DAWSONIA Nicholson

As the material referable to Dawsonia which has been found at the Deep kill is considerably larger and of a more varied nature than that of Caryocaris, it allows a more positive identification and expression of opinion on the taxonomic relations of these bodies.

Nicholson [*loc. cit.*] proposed the name Dawsonia for the "ovarian vesicles" of graptolites which he had described in his *Monograph of British Graptolites* [pt 1, p.71, fig.4] and which he later on[1] designated as "gonangia" of graptolites. He described four species, viz D. acuminata,

[1] Nicholson & Lyddeker. Manual of Paleontology. 1889. 1:214.

D. rotunda, D. tenuistriata and D. campanulata. The first three are cited from the Point Levis shales of Quebec, the fourth from the Upper Llandeilo of the south of Scotland. The last species is very common in the Trenton (Normanskill) graptolite slates of New York and Canada and will be noticed in the description of the Trenton graptolite fauna. Nicholson's second and third species, which are also very common in the Deep kill slates, are, without doubt, leached out shells of small undescribed brachiopods, referable to Acrotreta and Paterula. The first species, D. acuminata, which is the genotype, is represented by long, oval, corneous bodies, which have one extremity prolonged into a long acuminate mucro. The genus, originally proposed for an agglomeration of variously shaped bodies, belonging to entirely different groups, should evidently be restricted to fossils of similar form and character.

Nicholson's contention that these fossils were gonangia of graptolites has never found any recognition, and this for good reason; for, while they are found associated in great numbers with the graptolites and only with these, they have never been observed in direct attachment to any part of the rhabdosome, but are always found entirely free. Their mere association with the graptolites is no evidence of their being a part of the graptolite structure; just as little the minute brachiopod shells,[1] mostly of oboloid type and found often in immense numbers associated with graptolites, would be considered as parts of graptolites.

As these fossils have not been considered to be of graptolitic nature, we do not find them cited in the lists of graptolites, as for instance in those of the Skiddaw or of the St David's shales. Lapworth mentions D. campanulata in his *Catalogue of the Western Scottish Fossils* [p.7]; but among the crustaceans. Ami [1889, p.117k] cites three forms of Dawsonia with

[1] The brachiopods of the graptolite shales are, from the Cambric shales to the Utica epoch, so similar in all their characters that, while belonging to different genera, they probably furnish an excellent instance of adaptation to a definite mode of life — perhaps a pseudoplanktonic existence by adhesion to floating seaweeds. They will, at an opportune time, be made the subject of a separate investigation by the writer.

the graptolites of the St Lawrence region. With these exceptions, these extremely common fossil organisms of the graptolite shale remained completely unnoticed till Dr Gurley began systematically to study the North American graptolites. He recognized two species in the Beekmantown shales of Point Levis, Quebec, both of which are found in the homotaxial Deep kill beds.

In one of them, D. tridens, its author observed three denticles, which, he states, "seem to indicate thecae, but from the extreme tenuity of the film it is not possible to determine this point definitely." Our examples of the same species show these same pointed denticles very distinctly in some cases [pl.17, fig.19]. While they appear as nothing but incisions into the margin of the fossil — which, however, by their regularity and sharp delineation seem to refute the supposition that they could be a mere fringing out of the margin due to the cleavage of the rock — we are able to discern distinct, projecting thecae in several well preserved specimens of the other species, D. monodon [fig.23]. They are also shown in profile in a fragment of the apical part of the latter species and exhibit in the frontal view transversally oval apertures [pl.17, fig.25].

These observations suggest that at least the two species of Dawsonia noted in this place, were provided with a small number of thecae. The bodies described here appear to represent the perfect organism, as they are clearly and definitely bounded at both extremities. As colonies, they look very different indeed from all other graptolite colonies, and they must, if they should be proved by further investigations to be complete, be regarded as a quite aberrant branch of the class of graptolites.

The carbonaceous films, representing these two species of Dawsonia, have, above all, the appearance of having originally belonged to bag-shaped bodies. This impression is specially created by wrinkles which run parallel to and increase toward the major margins [comp. fig.24]. As these supposed bags do not show any indications of attachment at either end, it is to be inferred that the colonies remained free during their lifetime, and the major portion of the bags may have functioned as hydrostatic apparatus.

### Dawsonia tridens Gurley

Plate 17, figure 18-20

Dawsonia tridens Gurley. Jour. Geol. 1896. 4:88, pl.5, fig.5
Dawsonia tridens Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.556

*Description.* Rhabdosome shortly and asymmetrically fusiform in outline; about 3 mm long (3.4 mm maximal length observed), 1.1mm wide, drawn out at both extremities into blunt mucros. A median groove, which becomes most distinct at the athecal extremity, connects the mucros. On one side there are two or three oblique incisions which produce acute denticles of the appearance of thecae. Other side more convex, with entire margin. Substance chitinous (?), thin.

*Position and localities.* Common at the Deep kill in graptolite beds 1 and 2 of the Tetragraptus horizon. Gurley obtained his types from the same horizon at Point Levis.

*Remarks.* Our material agrees in most particulars with the description and figure given by Dr Gurley. We were, however, unable to discern the "pustules" observed by him at the inner ends of the incisions; but noticed sometimes a widening of the incisions at this place [fig.18]. The groove, described by the same author, as occurring at the blunter extremity, crosses our specimens longitudinally. As Gurley remarks, this species resembles in outline and size most closely D. acuminata Nicholson. The latter, however, has one extremity rounded and can by this feature be readily distinguished.

### Dawsonia monodon Gurley

Plate 17, figure 21-26

Dawsonia monodon Gurley. Jour. Geol. 1896. 4:88, pl.5, fig.4
Dawsonia monodon Ruedemann. N. Y. State Paleontol. An. Rep't. 1902. p.554, 556

*Description.* Rhabdosome elongate rhomboidal in outline; about 10 mm long and 3 mm wide; of the two extremities of the major axis one (proximal one?) rounded, the other acutely tapering; the two lateral extremities extended into shorter, downwardly directed mucros. The acutely tapering

apical extremity theciferous, three to four tubular thecae, directed away from the apex, inclined at an angle of about 20°, four times as long as wide, in contact about one half of their length, outer margin slightly concave, apertural margin normal to the axis of the theca. Sicula not observed.

Fig. 105 Dawsonia monodon Gurley. From the Beekmantown shales at Point Levis, Canada. x1.5 (Copy from Gurley)

*Position and localities.* Common in graptolite beds 1 and 2 of the Deep kill zone with Tetragraptus; at Point Levis in the same horizon.

*Remarks.* The term, monodon, is a misnomer, for the long apical tooth is flanked by two lateral teeth. In Dr Gurley's specimen one of these has, as the figure indicates, been broken away, thus leading to the misconception. The remaining lateral mucro has apparently been taken by the author of the species for a denticle, representing a theca. Our material, however, demonstrates [fig.23] that the thecae are to be found on the narrow, tapering lower extremity.

There extends on the film a broad and low, but well defined ridge longitudinally from the theciferous tapering end to near the blunt, upper end. This appears to be enveloped by a gradually widening conical mantle, proceeding or suspended from the rounded upper end and terminating below the middle, its lower margin being produced into the lateral mucros. The whole has the appearance of a single theciferous branch, extending the whole length of the organism and protruding at the lower (distal) end, the upper (proximal) portion of which is, (on all sides?) surrounded by a conical bag. As the rhabdosome does not show any indications of having been attached in any way, it would here, as in the preceding species, suggest itself that the bag represents some form of hydrostatic apparatus.

A difficulty to the understanding of this form is presented by the direction of the thecae away from the distal point or apex. This direction of growth appears identical with that in the Axonophora, but in the latter the sicula is always to be found at the farthest ends of the rhabdosomes, from which the thecae then grow in a backward direction toward the center of the colony. In the present species, however, nothing that would be comparable to a sicula is to be found at the supposed farthest theciferous end.

## SUPPLEMENTARY NOTES

**Note 1** Several pamphlets received from Mr T. S. Hall of Melbourne, when this memoir was nearly through the press, have given the writer the first intimation of important investigations on Lower Siluric graptolites carried on by our antipodes since the publications of McCoy and Etheridge on this subject. Unfortunately I have even now been unable to obtain all desired literature in time for this supplementary note. Since, however, the occurrence of our Beekmantown graptolites in Australia has, in this memoir, been recorded only after the identifications contained in the earlier papers, which, according to Mr Hall are — owing to their antedating Lapworth's revision of the British graptolites — in many cases unreliable, I append here in amendment of my oversight a list of the American graptolites recognized by Hall and others in Australia as well as other facts of importance from their papers in regard to the fauna here described.

The following list of later Australian publications, as complete as I can glean it from Mr Hall's papers, is to be added to "References," forming chapter 1.

1886 **Hector, James.** Catalogue New Zealand Geological Exhibits, Ind. and Col. Exhibit, p.82
1892 **Hall, T. S.** Proceedings Royal Society of Victoria. n. s. 4, p.7
1894 ——— ——— 6, p.74
1895 ——— ——— 7, p.55
1895 **Pritchard, G. B.** Proceedings Royal Society of Victoria. n. s. 7, p.30
1897 **Hall, T. S.** Proceedings Royal Society of Victoria. n. s. 10 [9 ?], p.131, 183
1897 **Dun, W. S.** Records of the Geological Survey New South Wales, 5:124
1898 **Hall, T. S.** Proceedings Royal Society of Victoria n. s. 10, p.202
1899 ——— ——— 11, p.164
1899 ——— Geological Magazine n. s. Dec. 4, 6:438

Mr Hall recognizes four divisions in the lower Ordovicic rocks of Victoria.

1 *Lancefield series*, which besides Australian species of Bryograptus, Leptograptus, Didymograptus, Tetragraptus, a Phyllograptus? and Dictyonema contains the following species of the Northern Hemisphere.

Clonograptus flexilis *J. Hall*
C. rigidus *J. Hall*
C. rigidus *var.* tenellus *Linnars.*

2 *Bendigo series.* This contains the following species[1]:

*Didymograptus bifidus
D. *cf.* decens *Törnq.*
*D. gracilis *Törnq.*
*D. caduceus *Salter*
*Tetragraptus fruticosus *J. Hall*
*T. serra *Brong.*
*T. quadribrachiatus *J. Hall*
*Dichograptus octobrachiatus *J. Hall*
*Phyllograptus typus *J. Hall*
*Goniograptus thureaui *McCoy*
G. macer *T. S. Hall*

3 *Castlemaine series.* This contains:

*Didymograptus bifidus *J. Hall*
D. murchisoni *Beck* (a European form)
D. *cf.* decens *Törnq.* (a European form)
*D. caduceus *Salter*
*Tetragraptus serra *J. Hall*
*T. quadribrachiatus *J. Hall*
T. projectus *T. S. Hall*
*Dichograptus octobrachiatus *J. Hall*
*D. octonarius *J. Hall*
*Clonograptus *sp.*
*Phyllograptus typus *J. Hall*
*P. angustifolius *J. Hall*
*Loganograptus logani *J. Hall*
Goniograptus macer *T. S. Hall*
Dendrograptus *sp.*
Diplograptus *sp.*
Climacograptus *sp.*
Trigonograptus *sp.*? and other unidentified forms

4 *Darriwill series.* The fauna of this series is said to differ from the Castlemaine one by the almost entire absence of Didymograptus caduceus and the appearance of Lasiograptus and Glossograptus; Trigonograptus and several species of Didymograptus and Climacograptus occur, while Tetragraptus serra and Loganograptus still persist.

A comparison of these fossil lists with those from New York and Canada leaves no doubt that the general sequence of the American and the Victorian graptolites is the same, but as Mr Hall states "experience has shown that it is unsafe to push the analogy too far and that the only safe method is that of detailed stratigraphic work." It is added by the same author: "Thus we find forms here associated which elsewhere are separated by intervening zones; and on the other hand, forms elsewhere associated may be here separated." In this connection it is now extremely interesting

[1] Those occurring in Canada or New York are denoted by an asterisk (*).

to note that the most important differences between the sequence of the graptolites of Australia and that of the northern hemisphere, pointed out by Mr Hall, are not borne out by the vertical distribution of the graptolites observed in New York, and the Australian and New York graptolite ranges agree in these cases. Didymograptus bifidus is stated to die out in Australia long before Phyllograptus typus has disappeared, but also at the Deep kill, where both continue through graptolite bed 5, the former passes its maximum frequency long before the latter. In the lowest Ordovicic rocks at Lancefield in Victoria "Clonograptus flexilis and C. rigidus are found in association with Bryograptus, while in Europe and America Byrograptus is a Cambrian form." At the Deep kill we have found two species of Bryograptus, one in great number, in a horizon undoubtedly still above that characterized by Clonograptus flexilis and C. rigidus. Loganograptus in Australia does not appear till Phyllograptus typus and closely allied species have become extinct. This is probably exactly the case in the graptolite beds of New York, where entire specimens of Loganograptus logani have only been found in the horizon with Diplograptus dentatus, though detached branches found in deeper horizons have been doubtfully referred to that species [*see* p.632], and Gurley also records the form only from the uppermost Levis horizon.

Since the exact faunules of the graptolite zones at Point Levis in Canada have not been determined and Gurley [1896, p.294] for instance is unable to state the range of Phyllograptus typus at that renowned locality, the sequence furnished by the Deep kill section in New York is at present to be considered as representing that of eastern North America. The differences pointed out by Mr Hall are then perhaps more those between the Australian and North American graptolite fields on one hand and the European on the other, or those between the Pacific and Atlantic basins.

There is no doubt that Mr Hall is right in placing the Lancefield series with its Clonograptus-Bryograptus fauna at the base of the Australian

graptolite beds, since our evidence goes to show that also here this fauna precedes the Tetragraptus-Phyllograptus fauna. From his statement that Didymograptus bifidus is very rare in the Bendigo series and "perhaps indicative of the higher beds of the series" I infer that in time the division line corresponding to that between our Tetragraptus zone and the zone with Didymograptus bifidus will be drawn through the Bendigo series, and likewise a division line between the latter zone and that of Diplograptus dentatus may be found in the Castlemaine series, and a very exact correlation of the American and Australian zones will thus be attained. At any rate so much is certain: that all the American zones of the Lower Ordovicic are represented in Australia. The number of forms common to America and Australia, which appear in Mr Hall's lists, is truly astonishing and will rather increase, I believe, as investigation proceeds.

Mr Hall adds to the few Lower Ordovicic forms cited by Frech [1897] from New Zealand Didymograptus bifidus, of which he has examples from Nelson, N. Z.

**Note 2** On page 517 of this memoir allusion is made to the description of an observation on the structure of the central disk of Dichograptus octobrachiatus which has been omitted in its proper place. In the example figured on plate 9, figure 1, the central disk has been split through the median plane in the separation of the slabs. On one slab a strong carbonaceous (chitinous) test is shown, on the other a calcareous layer, which rests on another carbonaceous test and clearly has segregated between the two carbonaceous tests. This calcareous layer is thickest between the branches and thins out toward the margin of the disk and upon the branches without, however, becoming everywhere discontinuous along the median line of the latter. The presence of this intercalated cake of carbonate of lime indicates that there must have existed either a space open long enough within the central disk to allow the segregation of the carbonate of lime, or at least an original plane of separation between two tests, where the deposition of the calcareous salt could take place. The form of the calcareous layer is such as to suggest the presence of an original open space in the disk, but at any rate the occurrence indicates the composition of the central disk of two tests.

# EXPLANATION OF PLATES

PLATE 1

## Genus DICTYONEMA Hall

*See* pl.3

## Dictyonema flabelliforme Eichwald (sp.)

Page 599

1-19 Astogenetic growth stages

1 Sicula with very long nema. x5

2 Sicula with budding first theca. x5

3 Sicula and first theca matured, showing the divergence of the latter. x5

4 *Idem*, from the other side, showing the origin of the first theca near the apex of the sicula. x4½

5 Young colony with two thecae. x5

6 Another view of a like growth stage in which both thecae strongly diverge. x5

7 A specimen of the same growth stage showing the point of origin of the second theca. x5

8 A young colony (rhabdosome) with three thecae, two of which appear to be of composite nature. x5

9 Another aspect of a like stage showing also the composite nature of one of the thecae. x5

10 Young rhabdosome with nema and primary disk. x5

11 Young rhabdosome in which the first dichotomy of a branch has taken place. x5

12 Young rhabdosome showing several bifurcations, the further growth of the branches and the form of the thecae. x5

13 A little more advanced rhabdosome with the first dissepiment. x5

14 Young colony seen from the under or theciferous side, exhibiting the thecal apertures. x5

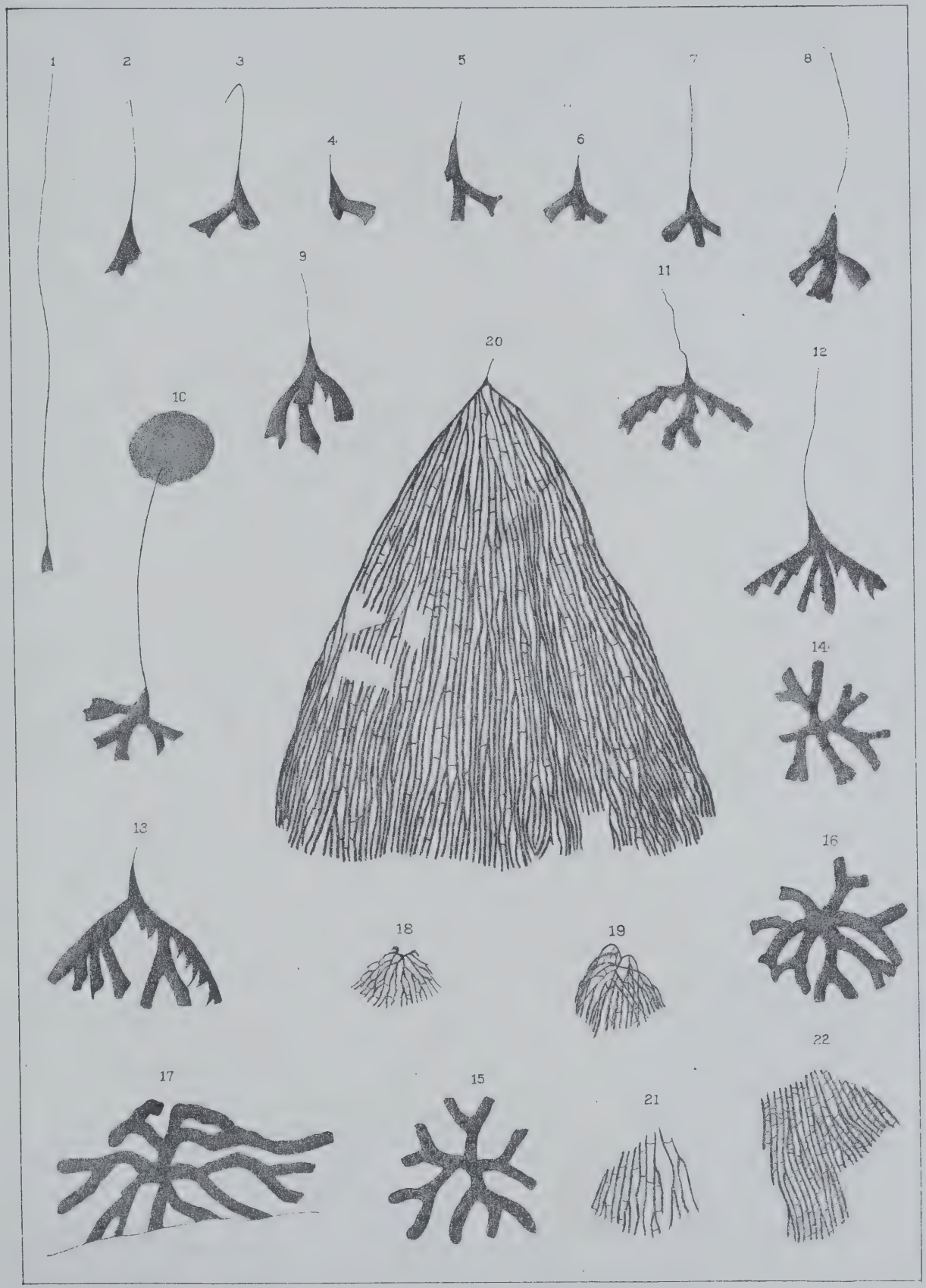
15 Same view of a somewhat older rhabdosome. The aperture of the sicula is seen in the center. x5

16 Young rhabdosome seen from the upper side. x5

17 Same view of a somewhat older colony. x5

# GRAPTOLITES

Memoir 7. N.Y. State Museum Plate 1




R. Ruedemann del. W.S. Barkentin lith.

18 Young, more advanced rhabdosome, compressed somewhat obliquely and thereby showing the cruciform initial portion and the absence of dissepiments in the latter

19 Same view of a still more advanced rhabdosome which shows a somewhat abrupt downward bending of the branches

20 Normal and approximately mature specimen

21 Fragment of a variety with widely separated branches and dissepiments and closely arranged thecae

22 Fragment of the opposite extreme of variation with closely arranged broader branches and dissepiments (var. confertum)

All specimens are from the upper Cambric Dictyonema shale at Schaghticoke, Rensselaer co. N. Y. The originals are in the New York State Museum.

PLATE 2

## Genus STAUROGRAPTUS Emmons

## Staurograptus dichotomus Emmons

Page 614

1–13 Growth stages

1 Sicula with nema and primary disk; the latter shaded much too dark in proportion to the thickness of its test. x5

2 Sicula showing aperture and fragment of primary disk. x5

3 Sicula with budding first theca. x5

4 Sicula with long nema, matured first and budding second theca. x5

5 Young rhabdosome with fragmentary primary disk and three thecae. x5

6 Young rhabdosome in which the coenosarcal cavities have been filled with pyrite and are plastically preserved. The point of gemmation of the first and second theca and the formation of the four secondary branches by bifurcation are distinctly shown. The latter takes place so close to the sicula that apparently four branches spring from the latter [*see* fig.7–10]. x5

7 Somewhat obliquely compressed young rhabdosome which shows the first bifurcation of a secondary branch and the succeeding thecae of the branches. x5

8 Frontal view (or rhabdosome, seen from below) of a somewhat younger stage showing the aperture of the sicula in the center. x5

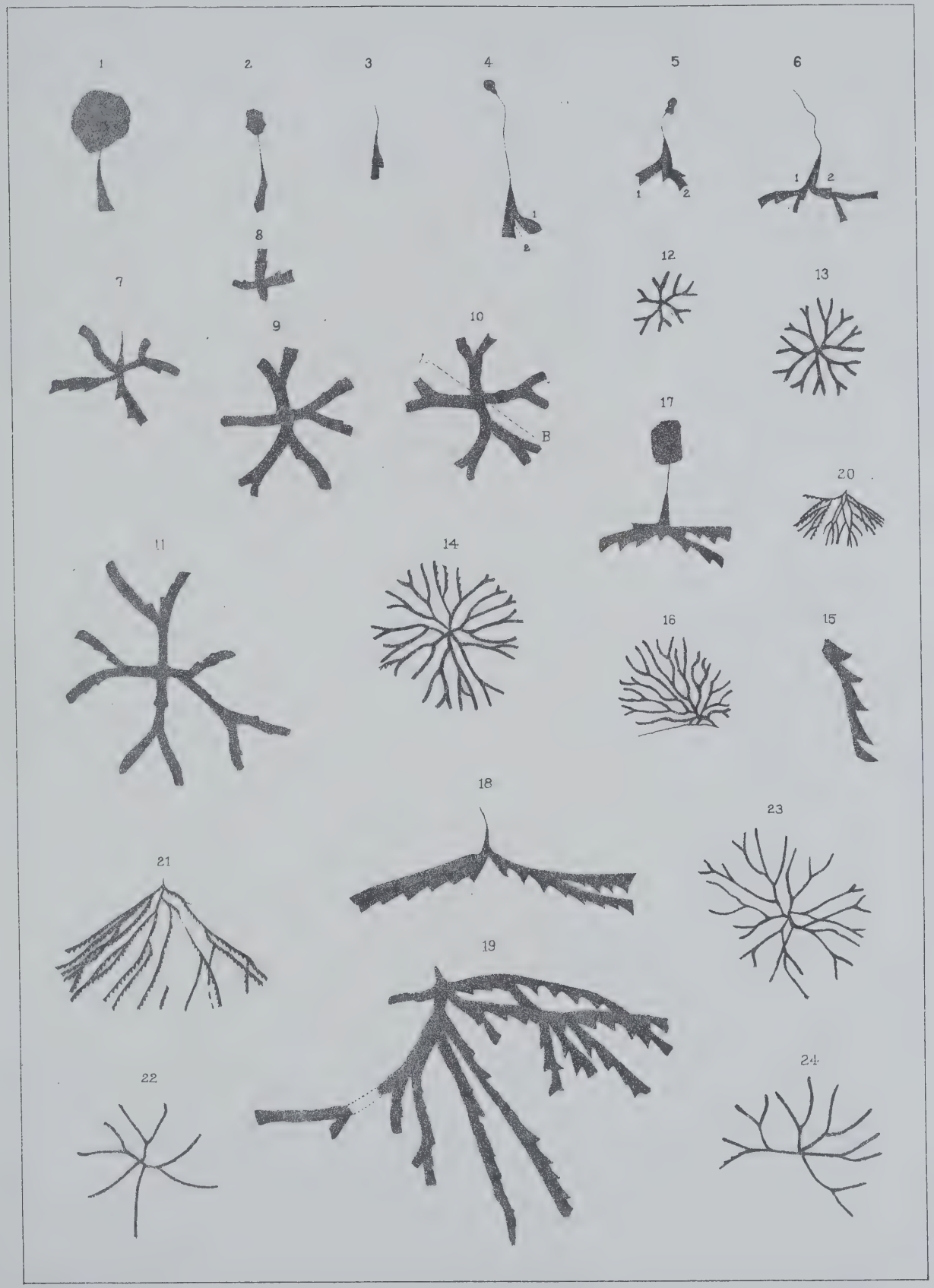
9 Like view of an older growth stage in which three of the four secondary branches have divided by dichotomy. x5

10 Like view of a still more advanced stage in which all four secondary branches have again become bifurcated and one begins to form branches of the fourth order. The form described by Emmons as Staurograptus dichotomus was a growth stage but slightly less advanced than this. x5

11 Same view of a stage which exhibits an unequal development of the four secondary branches. x5

# GRAPTOLITES






R. Ruedemann del. W.S. Barkentin, lith.

12 Young rhabdosome with branches of a higher order
13 Still more advanced rhabdosome
14 Specimen in the mature condition
15 Lateral view of a portion of a mature branch. x4½
16 Fragment of a colony exhibiting an undulating character of the branches
17 A laterally compressed early growth stage, giving a lateral view of the early thecae and the bryograptoid aspect of the young colony. x5
18 The same view of a more advanced growth stage. x5
19 The bryograptoid aspect of an adolescent stage. x5
20 The same aspect of a young, dense form

**Staurograptus dichotomus** var. **apertus** var. nov.

21 The bryograptoid aspect of a mature, loosely branched form with few bifurcations
22 A variety with extreme scarcity of branching
23 A mature specimen with moderately scarce branching and widely diverging branches
24 A specimen with extremely widely divergent branches and scarce bifurcation

All specimens are from the upper Cambric shales at Schaghticoke, Rensselaer co. N. Y. The originals are in the New York State Museum.

PLATE 3

## Genus DESMOGRAPTUS Hopkinson

### Desmograptus intricatus sp. nov.

Page 611

1 Fragment of long conical rhabdosome

2 Nearly perfect rhabdosome showing at the left side a fragment of the lower layer of the compressed cone

3 Fragmentary rhabdosome with very small meshes

4 Broadly conical rhabdosome

Graptolite bed 7 of the Deep kill section. Figures 1–4 are incorrectly reproduced. The meshes should be twice as close. (*See* text figure 30, 32)

### Desmograptus cancellatus Hopkinson

Page 610

5 Fragment of rhabdosome with somewhat elongate meshes

6 Fragment with shorter meshes

7 Fragment of rhabdosome showing character of proximal and distal branches and meshes

8 Fragment with large and broad meshes

Graptolite bed 7 of the Deep kill section, Rensselaer co. N. Y.

## Genus DICTYONEMA Hall

*See* pl. 1

### Dictyonema rectilineatum sp. nov.

Page 607

9 Fragment of rhabdosome

10 Fragment of a more distal portion of the rhabdosome than shown in the preceding figure

Graptolite bed 7 of the Deep kill section

### Dictyonema furciferum sp. nov.

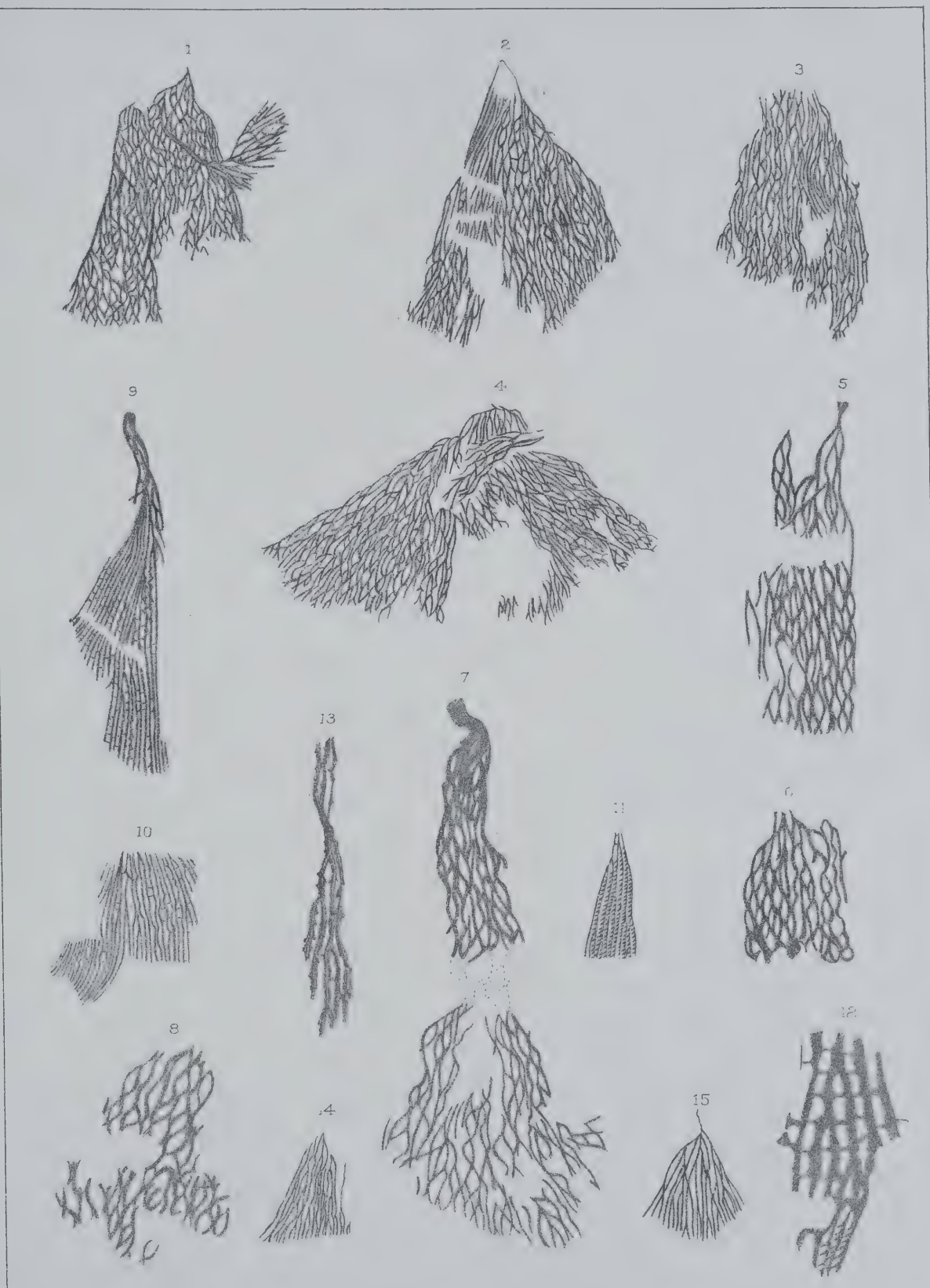
Page 606

11 Fragment of rhabdosome

Graptolite bed 2 of Deep kill section

# GRAPTOLITES

Memoir 7. N.Y. State Museum. Plate 3




R.R. et G.S.B. del. W.S. Barkentin, lith.

**Dictyonema murrayi** Hall

Page 606

12 Fragment of rhabdosome

Sandy shales at Defreestville, Rensselaer co. N. Y. Original in United States National Museum

Genus CALLOGRAPTUS Hall

**Callograptus salteri** Hall

Page 584

13 Fragment of rhabdosome showing the character of the thecae. x2

14 Young rhabdosome, exhibiting a somewhat undulating character of the branches

15 Another young rhabdosome with nemacaulus and more rigid character of branches

Graptolite bed 2 of the Deep kill section

PLATE 4

Genus DENDROGRAPTUS Hall

**Dendrograptus ? succulentus** sp. nov.

Page 581

1 Large rhabdosome
2 Younger rhabdosome
3 Fragment of rhabdosome showing long undivided branches
4 Fragment of rhabdosome showing terminal tufts of fine branches
Graptolite bed 7 of the Deep kill section

**Dendrograptus flexuosus** Hall

Page 579

5 Young rhabdosome
6 Young rhabdosome with closely arranged branches
Graptolite bed 2 of the Deep kill section
8 Young rhabdosome with basal disk or bulb. x2
9 Greater enlargement of the same to show the thecal apertures. x7
10 Fragment of rhabdosome, showing the thecae. x2
Graptolite bed 3 of the Deep kill section

**Callograptus** cf. **diffusus** Hall

Page 586

7 Fragment of young rhabdosome. x2
Graptolite bed 2 of the Deep kill section

**Dendrograptus fluitans** sp. nov.

Page 582

11 Rhabdosome. x2
12 Further enlargement of branch of same. x7
Graptolite bed 2 of the Deep kill section

Genus PTILOGRAPTUS Hall

**Ptilograptus tenuissimus** sp. nov.

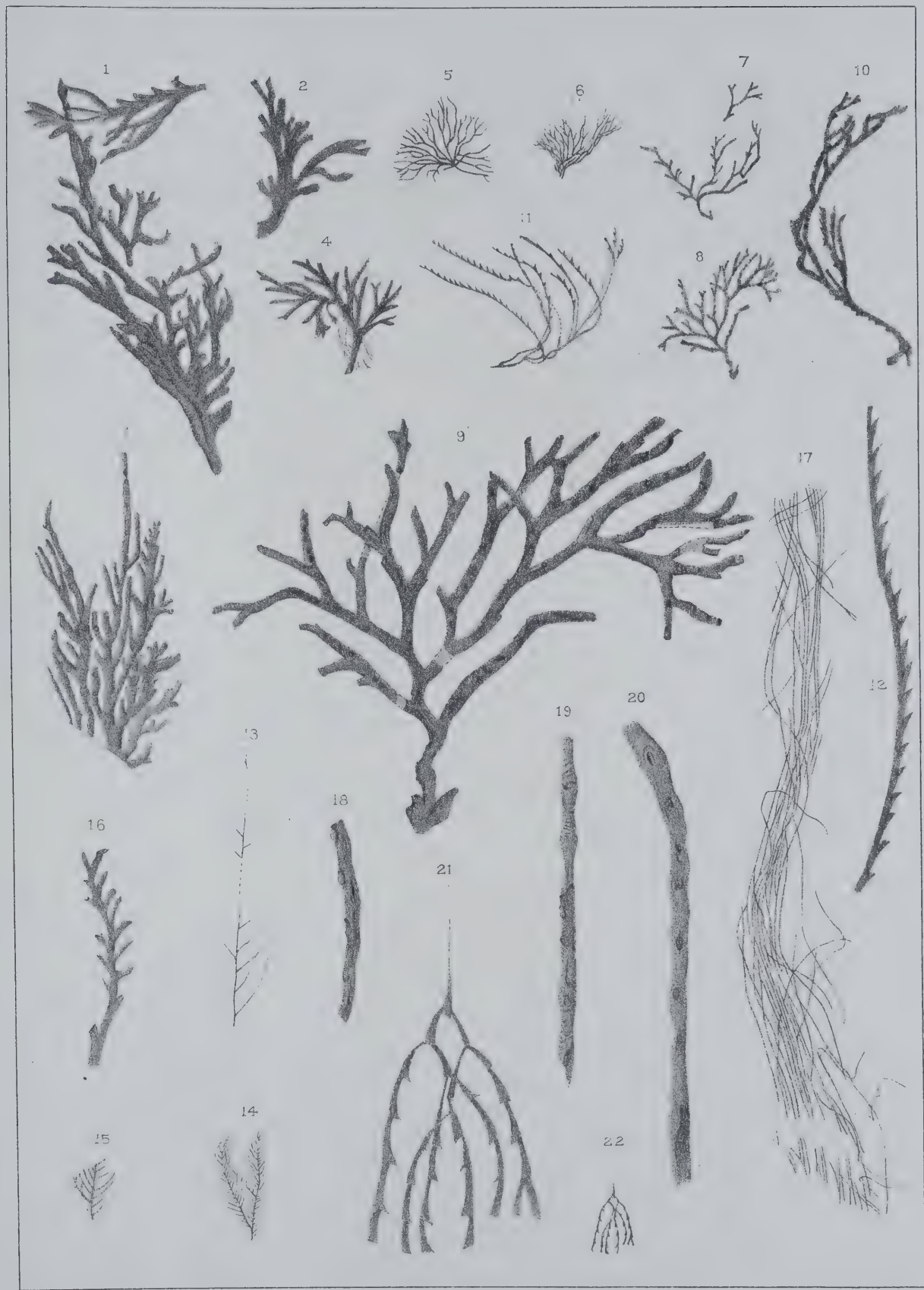
Page 591

13 Rhabdosome. x2
Graptolite bed 3 of the Deep kill section

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 4




R.R. et G.S.B. del.

W.S. Barkentin lith.

**Ptilograptus plumosus** Hall

Page 588

14 Rhabdosome

15 Fragment of rhabdosome. x2

Graptolite bed 7 of the Deep kill section

**Ptilograptus geinitzianus** Hall

Page 590

16 Enlargement of stem. x2

Graptolite bed 3 of the Deep kill section

Genus STROPHOGRAPTUS gen. nov.

**Strophograptus trichomanes** sp. nov.

Page 717

17 Bundle of branches

18–20 Enlargements of fragments of branches to show character of thecae. x7

Graptolite bed 7 of the Deep kill section

Genus BRYOGRAPTUS Lapworth

*See* pl. 5

**Bryograptus pusillus** sp. nov.

Page 641

21 Rhabdosome. x7

22 Same. x2

Graptolite bed 2 of the Deep kill section

PLATE 5

## Genus BRYOGRAPTUS Lapworth

*See* pl. 4

### **Bryograptus lapworthi** sp. nov.

Page 639

1 Young rhabdosome consisting of sicula and first two thecae, referred with doubt to this species. Shows apical origin of first theca. x8

2 Obverse side of young rhabdosome with two more thecae. Shows also apical origin of first theca. x8

3 Rhabdosome with four branches of the second order. x2

4 Rhabdosome with five branches of the second order

5 Rhabdosome with relatively small angle of divergence. x2

6 Rhabdosome with large angle of divergence. Branches of the second order are absent. x2

7 Rhabdosome with symmetric formation of branches of the second order. x2

8 Specimen with very large angle of divergence. x2

9 Very asymmetric rhabdosome. x2

10 Very large specimen with very distal formation of branches of the second order. x2

11 Enlargement to show the mode of bifurcation. x8

12 Young rhabdosome with nema and primary disk. x7

Graptolite bed 2 of the Deep kill section

## Genus SIGMAGRAPTUS gen. nov.

### **Sigmagraptus praecursor** sp. nov.

Page 702

13 Rhabdosome. x2

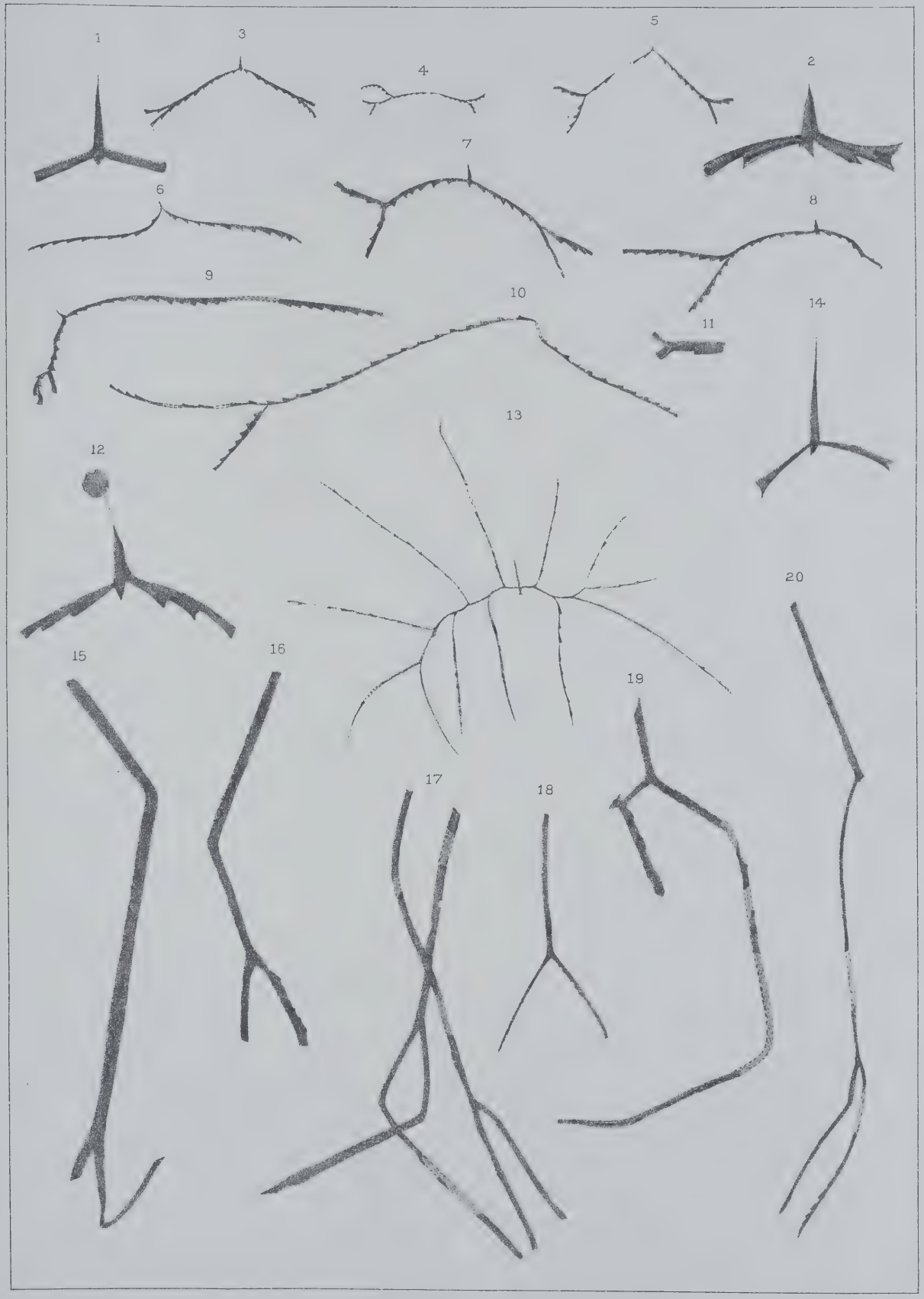
14 Sicula and first two thecae, presumably of this species. x7

Graptolite bed 3 of the Deep kill section

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 5




R.R. et G.S.B. del.

W.S. Barkentin lith.

Genus TEMNOGRAPTUS Nicholson

**Temnograptus noveboracensis** sp. nov.

Page 619

15–18 Branches, showing the dichotomous mode of branching

19 Central portion of rhabdosome

20 Distal branch

Graptolite bed 2 of the Deep kill section

PLATE 6

## Genus GONIOGRAPTUS McCoy

*See* pl. 7

### **Goniograptus thureaui** McCoy var. **postremus** var. nov.

Page 621

1–11 Astogenetic growth stages

1 Young rhabdosome consisting of sicula and first two thecae. x3½

2 Young rhabdosome, in which the branches of the first order have bifurcated, seen from the obverse side. x3½

3 A like growth stage seen from the reverse side. x3½

4 The next stage, in which the eight branches of the third order have formed. x3½

5 A slightly more advanced stage from the reverse side. The brachial thecae of the "denticulate branches" have commenced to form. x3½

6 A similar growth stage seen from the obverse side. x3½

7 A further growth stage of the rhabdosome, possessing the branches of the fourth order and short denticulate branches. x2½

8 Rhabdosome in an adolescent growth stage, in which the formation of the branches has proceeded to that of the eighth order and further growth consists in the lengthening of the denticulate branches. x2½

9 A somewhat more advanced growth stage showing the further longitudinal growth of the branches. x2⅓

10 A rhabdosome in which the formation of new branches has ceased, showing well the arrangement of the branches and the character of the four principal stems

11 Mature rhabdosome

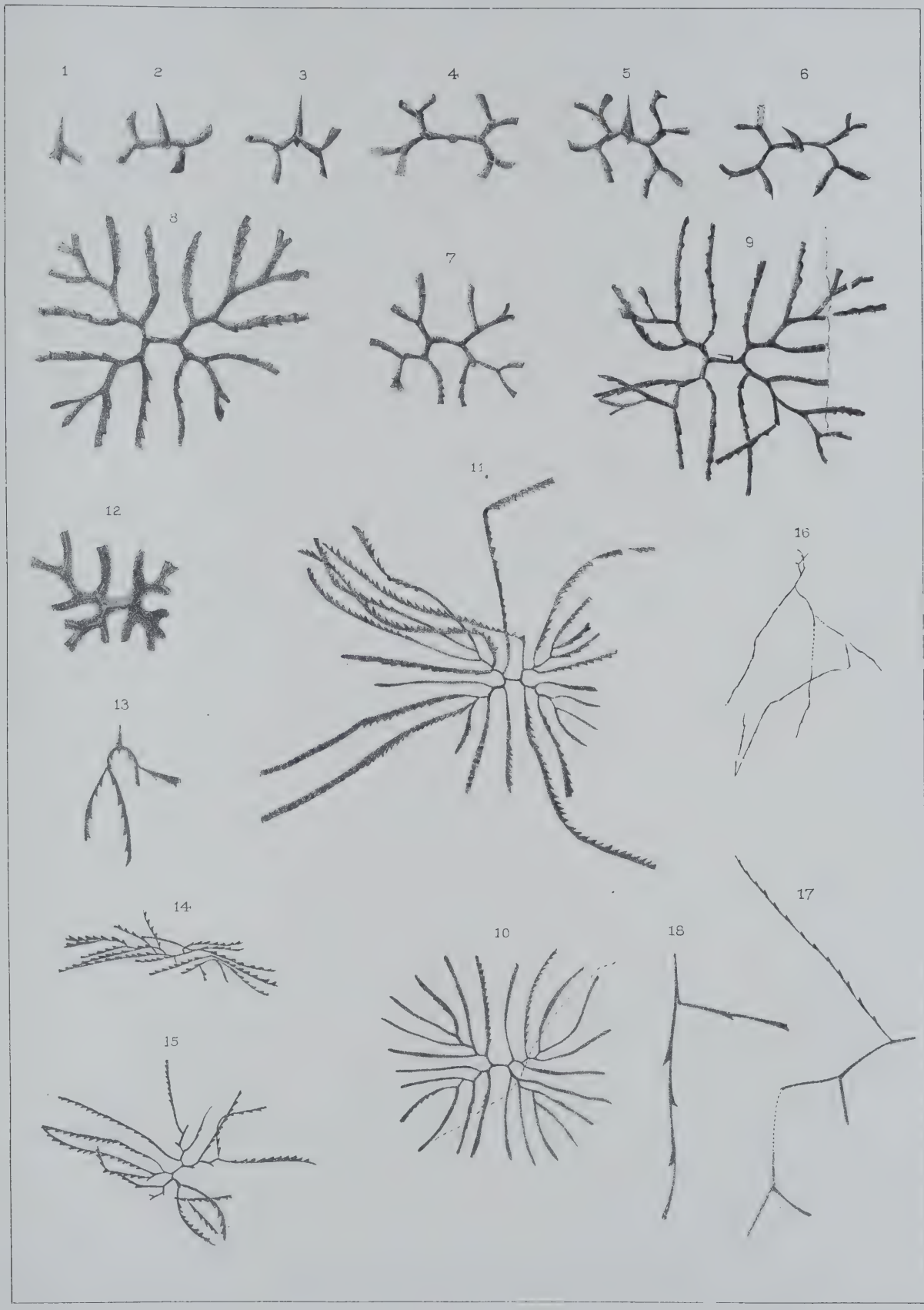
12 Central portion of a mature rhabdosome retaining the alate central disk. x2

13 A fragment of a rhabdosome. x2

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 6




R.R. et G.S.B. del

W.S. Barkentin, lith.

14 Rhabdosome which is laterally compressed, showing the horizontal disposition of the branches

15 A rhabdosome showing some irregularity of branching

All the originals are from graptolite bed 2 of the Deep kill section with the exception of that of figure 2, which is from graptolite bed 3.

**Goniograptus perflexilis** sp. nov.

Page 625

*See* pl. 7

16 Fragment of a rhabdosome

17 Fragment of a rhabdosome enlarged to show character of the thecae and of the stem internodes of the principal stem. x2

18 A further enlargement of a branch. x4½

The original of figure 17 is from graptolite bed 2 of the Deep kill section; that of figures 16 and 18 is from the exposure at Mt Moreno near Hudson N. Y.

PLATE 7

## Genus GONIOGRAPTUS McCoy

*See* pl. 6

### Goniograptus perflexilis sp. nov.

Page 625

*See* pl. 6

1 Young rhabdosome showing branches of first and second order. x2
2 Young rhabdosome with branches of the third order
3 Young rhabdosome with branches developed to the fourth order. x2
4 *Idem* in natural size
6 Mature rhabdosome in the usual confused state of preservation
7 About half of mature rhabdosome with the branches less confused
8 Restoration of a mature rhabdosome in spreading condition
9 Mature rhabdosome laterally compressed, retaining a proximal, apparently baglike appendage

Graptolite bed 2 of the Deep kill section

### Goniograptus geometricus sp. nov.

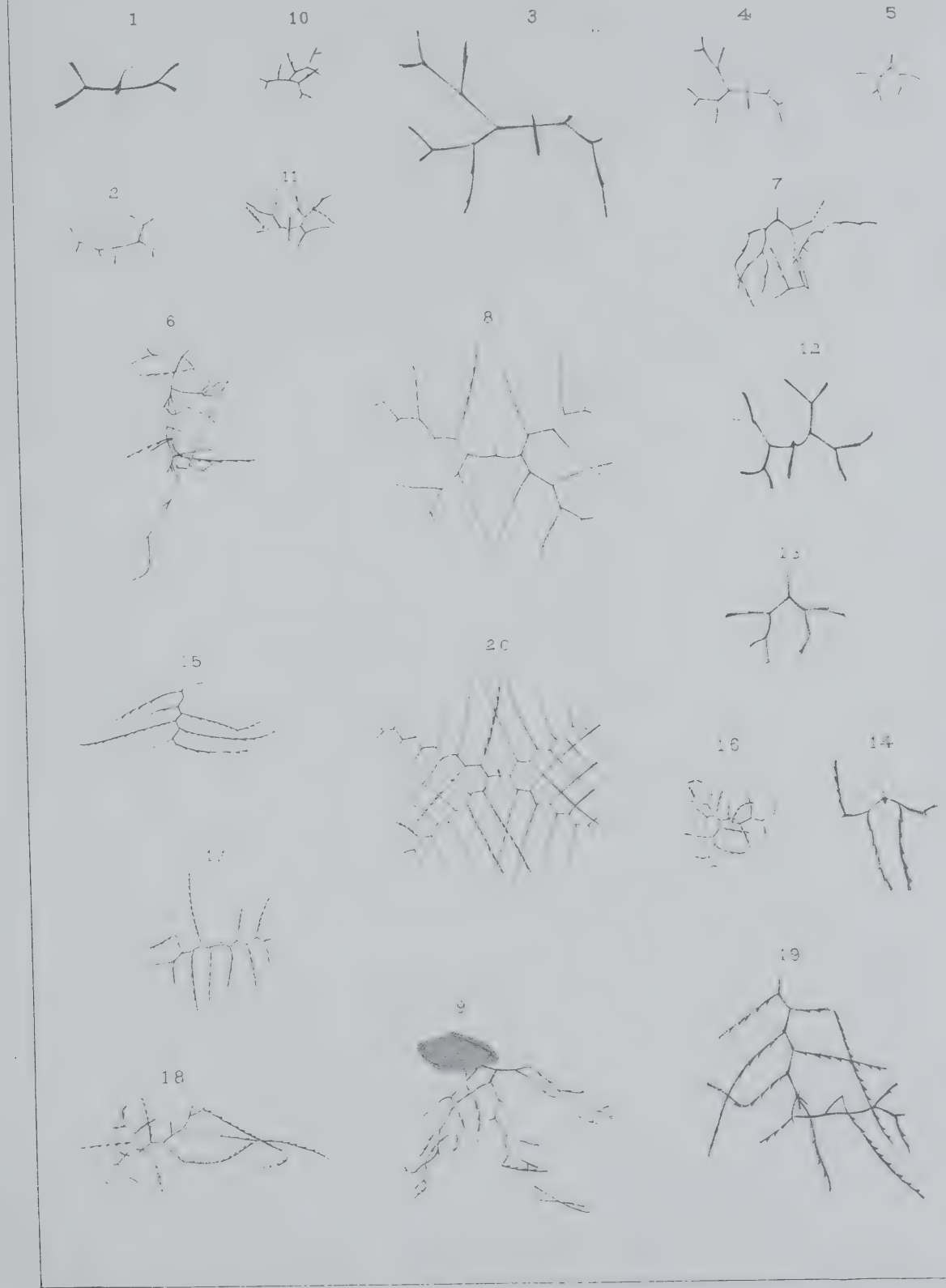
Page 627

5 Half of young rhabdosome
10 Young rhabdosome
11 Young rhabdosome with branches of the third order
12 Young rhabdosome in a similar stage of development. x2
13 Half of a young rhabdosome showing the points of origin of the denticulate branches. x2
14 Similar fragment with longer denticulate branches. x2
15 A principal stem and branches of a mature rhabdosome
16 Half grown rhabdosome showing the four principal stems
17 Two main stems with the lateral branches, the latter showing the angles of divergence in undistorted condition

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 7




R.R. et G.S.B. del.

W.S. Barkentin lith.

18 Fragment of mature rhabdosome showing the length attained by the branches

19 Principal stem with branches, enlarged to show the composition of the stem internodes of one theca each. x2

20 Restoration of a mature rhabdosome in undistorted condition

Graptolite bed 3 of the Deep kill section

PLATE 8

## Genus DICHOGRAPTUS Salter

## Dichograptus octobrachiatus Hall (sp.)

Page 634

*See* pl. 9

1 Young rhabdosome

2, 3 Rhabdosomes retaining the central disk

4 Mature rhabdosome

5 Fragment with central disk, showing the growth lines of the latter

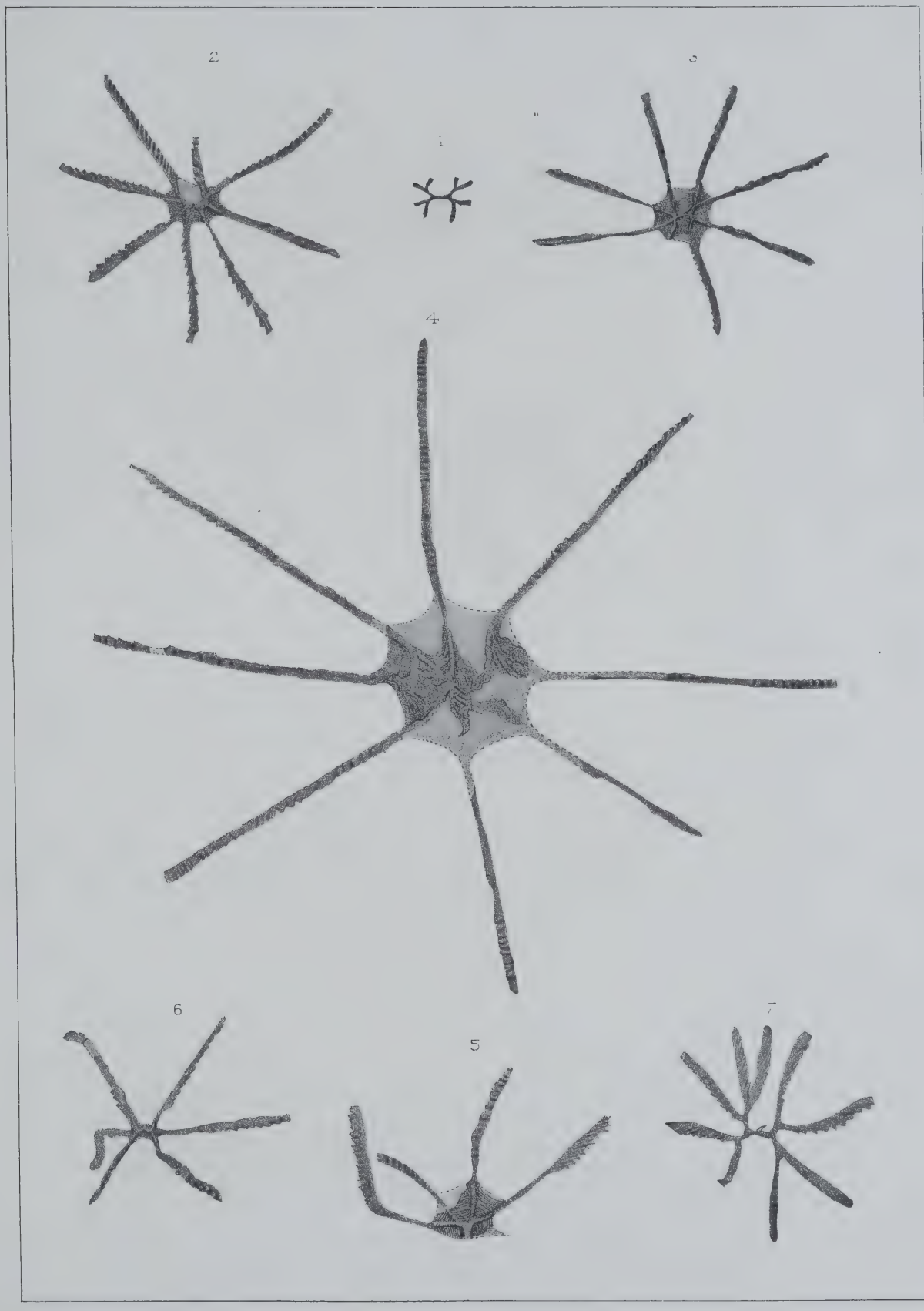
6 Rhabdosome in hexad stage of reduction

7 Specimen still retaining a bifurcation of the fourth order. x2

All originals are from graptolite bed 2 of the Deep kill section with the exception of that of figure 6, which is from graptolite bed 7.

# GRAPTOLITES






R.R. et G.S.B. del. W.S. Barkentin lith.

PLATE 9

## Genus DICHOGRAPTUS Salter

### **Dichograptus octobrachiatus** Hall (sp.)

Page 634

*See* pl. 8

1 Fragmentary rhabdosomes with mature disks
Graptolite bed 3 of the Deep kill section

2 Branch showing the thecae in their lateral aspect
Graptolite bed 2 of the Deep kill section

## Genus LOGANOGRAPTUS Hall

### **Loganograptus logani** Hall

Page 631

3 Young rhabdosome; its branches drawn too thick

4 Older rhabdosome

5 Rhabdosome with extremely tenuous branches

6 Central portion of a rhabdosome
All the originals are from graptolite bed 7 of the Deep kill section

## Genus TETRAGRAPTUS Salter

*See* pl. 10, 11, 12

### **Tetragraptus (Etagraptus) lentus** subgen. nov. et spec. nov.

Page 666

7 Rhabdosome

8 The same enlarged to show the character of the sicula and thecae. x2

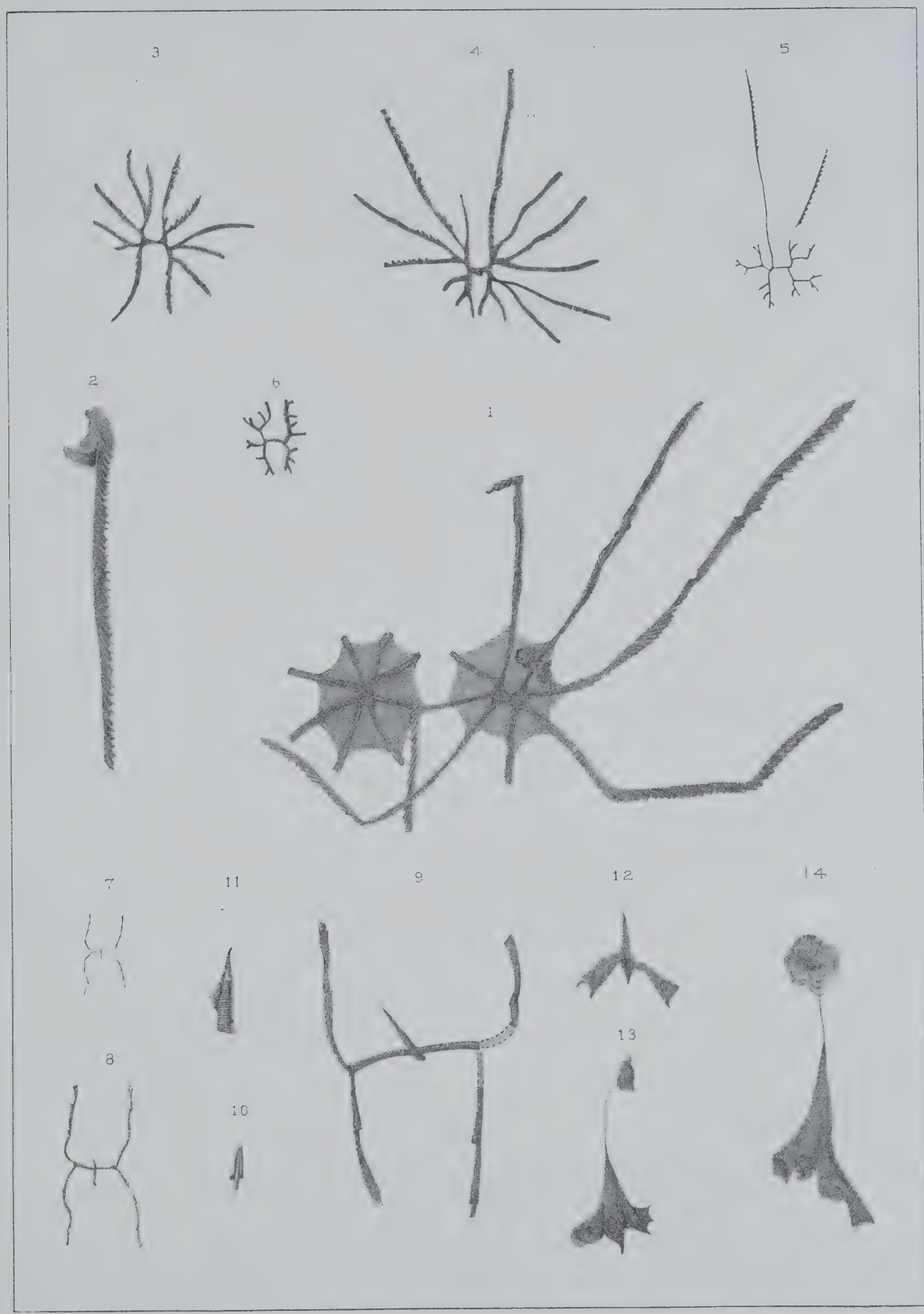
9 Another rhabdosome. x6½

10 Dorsal view of a theca. x6½
Graptolite bed 3 of the Deep kill section

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 9




R.R. et G.S.B. del.

W.S. Barkentin lith.

## Tetragraptus fruticosus Hall (sp.)

Page 649

*See* pl. 10

11 Sicula and first theca; pyritized. x7

12 Young rhabdosome consisting of sicula and first two thecae; obverse side. x7

13 Early growth stage of rhabdosome, retaining nema and a portion of the primary disk. x7

14 Young rhabdosome preserved in relief; shows the apical origin of the first theca, the growth direction of the first thecae, the sicula in obverse aspect, nema and primary disk. x8

All the originals are from graptolite bed 2 of the Deep kill section with the exception of that of figure 11 which is from bed 3 and is doubtfully referred to this species.

PLATE 10

## Genus TETRAGRAPTUS Salter

*See* pl. 9, 11, 12

## Tetragraptus fruticosus Hall (sp.)

Page 649

*See* pl. 9

1 Young rhabdosome in which the branches have not yet commenced to recurve

2, 3 Specimens with narrow, early recurving branches (var. tubiformis)

4 A well developed specimen with somewhat later beginning geniculation of the branches. Shows broad nema (nemacaulus)

5 Younger rhabdosome with the characters of var. tubiformis

6 A rhabdosome intermediate between the preceding and following forms. x2

7 Form with very late geniculation of the branches (var. campanulatus) and broad nema

8–10 Specimens with extremely late or imperfect recurving of the branches

Originals are all from graptolite bed 2 of the Deep kill section.

# GRAPTOLITES

Memoir 7. N.Y. State Museum. Plate 10

R.R. et G.S.B. del. W.S. Barkentin. lith.

PLATE 11

## Genus TETRAGRAPTUS Salter

*See* pl. 9, 10, 12

### Tetragraptus quadribrachiatus Hall (sp.)

Page 645

1 Young rhabdosome
Graptolite bed 2 of the Deep kill section

2 A young rhabdosome referred to this species
Graptolite bed 7 of the Deep kill section

3 Mature rhabdosome in which one of the branches has become laterally compressed, thus giving a lateral view of the thecae
Graptolite bed 2 of the Deep kill section

4 Common appearance and mode of preservation of the rhabdosomes in the shale
Graptolite bed 2 of the Deep kill section

### Tetragraptus amii Elles & Wood

Page 647

5 Typical mature rhabdosome

6 A younger rhabdosome showing the angle of divergence between the two pairs of branches

7 Young rhabdosome compressed laterally
Graptolite bed 2 of the Deep kill section

### Tetragraptus serra Brongniart (sp.)

Page 655

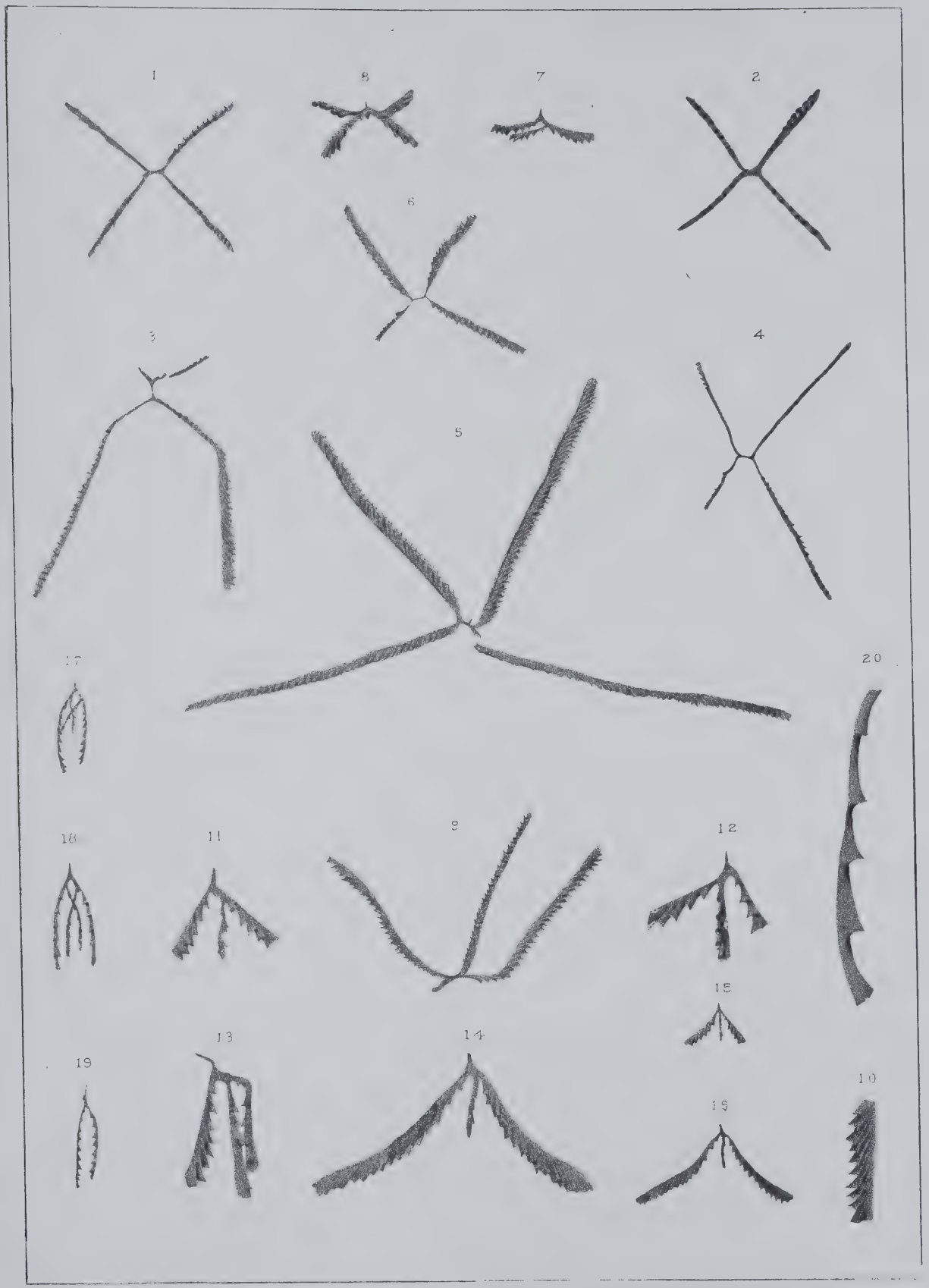
8 Young rhabdosome. x2

9 Average specimen

10 Enlargement of fragment of branch. x2
Graptolite bed 2 of the Deep kill section

# GRAPTOLITES

Memoir 7. N.Y. State Museum. Plate 11




R.R. et G.S.B. del. W.S. Barkentin. lith.

**Tetragraptus clarkei** sp. nov.

Page 652

11–13 Different aspects of young rhabdosomes. x2

14, 16 A mature rhabdosome, enlarged (x2) to show more distinctly the character of the thecae; and the same in natural size

15 Young rhabdosome, showing a rapid widening of the branches

Graptolite bed 3 of the Deep kill section

**Tetragraptus pendens** Elles

Page 653

17–19 Three different aspects of mature rhabdosomes; figure 18. x1½

20 Enlargement of fragment of branch. x6¼

Graptolite bed 3 of the Deep kill section

PLATE 12

## Genus TETRAGRAPTUS Salter

*See* pl. 9, 10, 11

### Tetragraptus woodi sp. nov.

Page 662

1 Young rhabdosome, which is so compressed that the angle of divergence of the branches of the second order is shown

15, 16 Two mature specimens

Graptolite bed 2 of the Deep kill section

### Tetragraptus similis Hall (sp.)

Page 658

2, 3 Two mature rhabdosomes laterally compressed and showing the common mode of preservation

4 A young rhabdosome spread out so that the branches of the first order are shown

Graptolite bed 2 of the Deep kill section

5 A mature rhabdosome compressed in such a way that two branches expose their lateral aspects in full width and two the frontal or dorsal sides

Graptolite bed 1 of the Deep kill section

6 A young rhabdosome showing well the proximal part and the rapid expansion of the branches. x2

7 A mature rhabdosome showing an uncommon mode of preservation by which the branches have become unnaturally divergent

8 Very early growth stage. Obverse side, showing the sicula and three thecae. x8

9 A little more advanced stage showing a long nema. Obverse view. x8

10 Young rhabdosome showing nema and primary disk. Only the two branches of one side exposed. x6½

Graptolite bed 2 of the Deep kill section

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 12

R.R. et C.S.B. del.

W.S. Barkentin lith.

**Tetragraptus pygmaeus** sp. nov.

Page 664

11 Young rhabdosome showing the long, narrow sicula and the four thecae from which the four branches grow. x5

12, 13 Obverse and reverse sides of two approximately matured rhabdosomes. x3.

14 Mature rhabdosome, reverse side. But two branches are exposed. x7

Graptolite bed 2 of the Deep kill section

**Tetragraptus taraxacum** sp. nov.

Page 663

17 Early growth stage of rhabdosome. Obverse side. x8

18 Mature rhabdosome. x2

19 Mature rhabdosome showing the rapid widening of the branches. x3½

20 Young rhabdosome, reverse side, further enlarged to show the point of origin of the first theca and the bifurcations. x7

21 Mature rhabdosome showing maximal length of branches observed. x2

22 The original of figure 19 in natural size

23 Rhabdosome showing the curvature of the branches. x2

24 Young rhabdosome showing the slender form of the proximal thecae. x7

25 A lateral pair of branches retaining their original angle of divergence. x7

26 Another pair of lateral branches compressed in different directions. They show distinctly the outline of the thecae. x7½

Graptolite bed 2 of the Deep kill section

PLATE 13

## Genus DIDYMOGRAPTUS McCoy

*See* pl. 14, 15

### Didymograptus nitidus Hall (sp)

Page 671

*See* pl. 14, fig. 5, 6

1 Large rhabdosome
2 Branch, obliquely compressed
3 Typical specimen
4 Rhabdosome with slightly declined branches
Graptolite bed 2 of the Deep kill section

### Didymograptus nitidus Hall, var. grandis var. nov

Page 674

5 Most perfect specimen observed
Graptolite bed 2 of the Deep kill section

### Didymograptus törnquisti sp. nov.

Page 688

6 Type specimen
7 Same, x1⅝, to show more distinctly the character of the thecae
Graptolite bed 3 of the Deep kill section

### Didymograptus patulus Hall (sp.)

Page 674

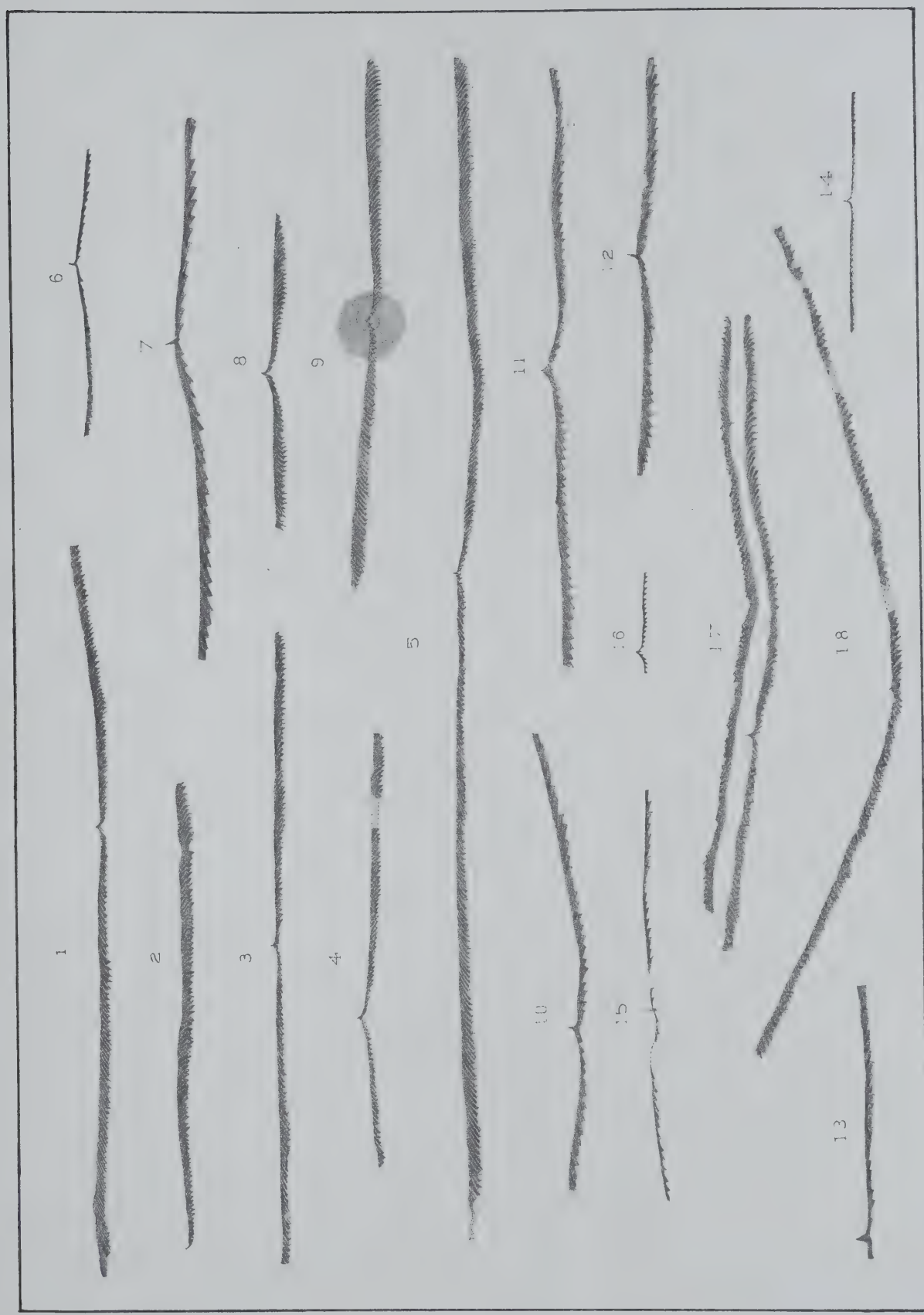
*See* pl. 14

8 Young typical specimen
9 Nearly mature specimen with central disk
Graptolite bed 2 of the Deep kill section

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 13




R.R.et G.S.B. del.

W.S. Barkentin, lith.

**Didymograptus nicholsoni** Lapworth, var. **planus** Elles & Wood

Page 685

10 Imperfect specimen with slightly reclined branches in the compressed state. Reverse side. x2

11 Typical rhabdosome. x1$\frac{8}{9}$

12 Young rhabdosome. Obverse side. x2

13 Specimen showing distinctly the origin of first theca. x2

14 Same in natural size

Graptolite bed 2 of the Deep kill section

**Didymograptus acutidens** Lapworth

Page 683

15 Characteristic rhabdosome. x1$\frac{9}{10}$

Graptolite bed 2 of the Deep kill section

**Didymograptus cuspidatus** sp. nov.

Page 684

16 Sole rhabdosome observed

Ash hill quarry at Mt Moreno, Columbia co. N. Y.

**Didymograptus extensus** Hall (sp.)

Page 668

*See* pl. 14

17, 18 Constrictiform appearance

Graptolite bed 2 of the Deep kill section

PLATE 14

## Genus DIDYMOGRAPTUS McCoy

*See* pl. 13, 15

### Didymograptus extensus Hall (sp.)

Page 668

*See* pl. 13

1, 2 Rhabdosomes showing the large size attained by this species
Graptolite bed 2 of the Deep kill section

3, 4 Young rhabdosomes with primary disks. The disks are shaded too dark. x2
Graptolite bed 1 of the Deep kill section

### Didymograptus nitidus Hall (sp.)

Page 671

*See* pl. 13

5–6 Young rhabdosomes with primary disks. The disks are shaded too dark. x2
Graptolite bed 1 of the Deep kill section

### Didymograptus patulus Hall (sp.)

Page 674

*See* pl. 13

7 Young rhabdosome with fragmentary primary disk. x2
Graptolite bed 1 of the Deep kill section

### Didymograptus filiformis Tullberg

Page 686

8–11 Various aspects of young rhabdosomes. x2
Graptolite bed 2 of the Deep kill section

12 Mature specimen
Graptolite bed 1 of the Deep kill section

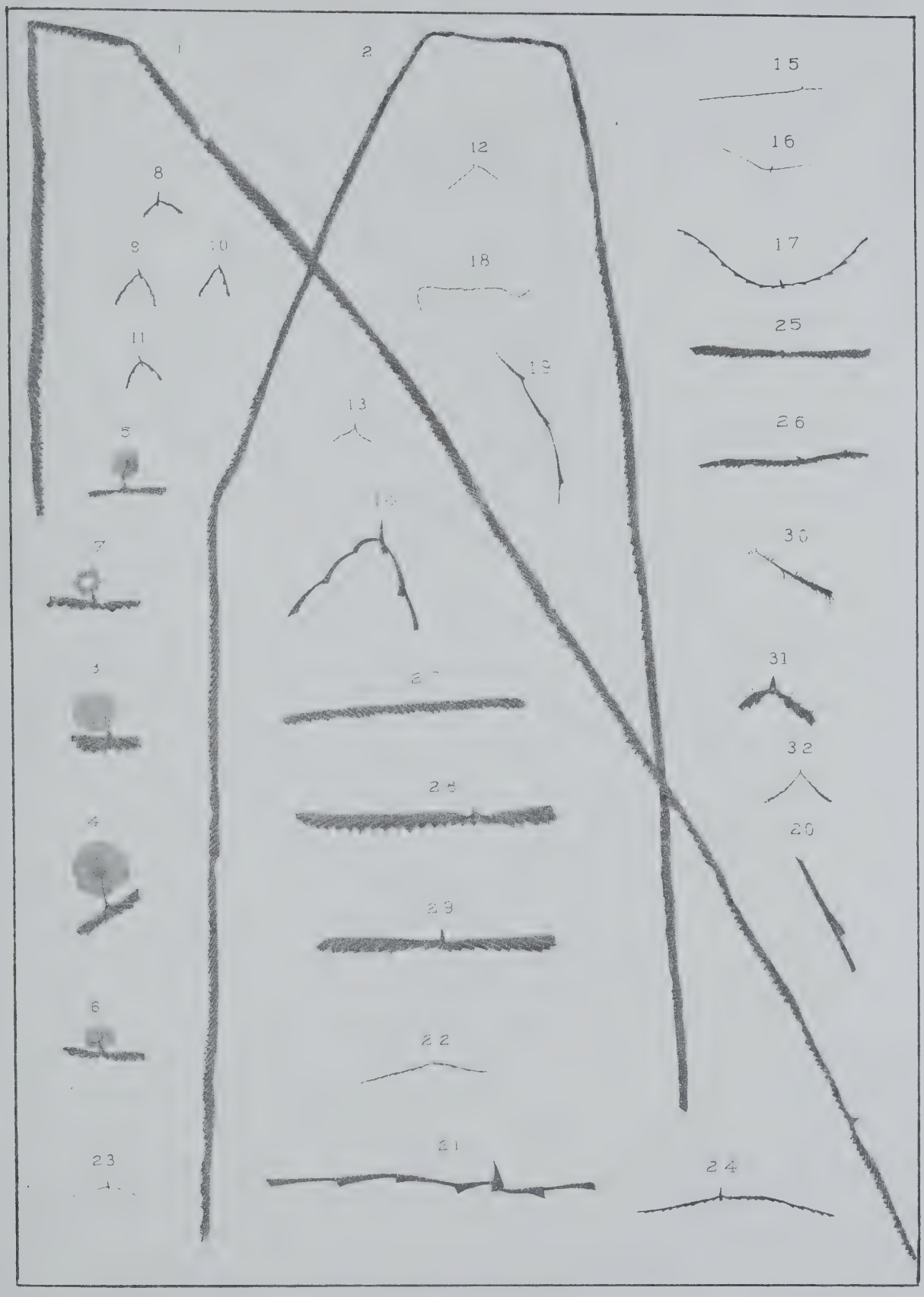
13 Rhabdosome
Ash hill quarry, Mt Moreno, Columbia co. N. Y.

14 Young rhabdosome; obverse side, x6½, to show character of sicula and thecae
Graptolite bed 2 of the Deep kill section

# GRAPTOLITES

Memoir 7 N.Y.State Museum

Plate 14




R.R.et G.S.B.del.

W.S.Barkentin,lith.

**Didymograptus gracilis** Törnquist

Page 679

15, 16 Mature rhabdosomes

17 Obverse side of rhabdosome. x2

Graptolite bed 3 of the Deep kill section

18 Relatively large specimen

Ash hill quarry, Mt Moreno, Columbia co. N. Y.

19 Distal portion of branch with extremely slender thecae. x6½

20 Another similar fragment. x8

21 Enlargement (x8) of proximal portion of rhabdosome, to show sicula and proximal thecae

Graptolite bed 3 of the Deep kill section

**Didymograptus ellesi** sp. nov.

Page 682

22, 23 Typical rhabdosomes

24 Rhabdosome. x2

Graptolite bed 3 of the Deep kill section

**Didymograptus similis** Hall (sp.)

Page 677

25 Typical specimen

Graptolite bed 3 of the Deep kill section

26 Proximal portion of rhabdosome

Ash hill quarry, Mt Moreno, Columbia co. N. Y.

27 Fragment of large rhabdosome, referred to this species

28 Proximal portion of rhabdosome. Obverse side. x2

29 Young rhabdosome. x2

Graptolite bed 3 of Deep kill section

**Didymograptus spinosus** sp. nov.

Page 688

30 Largest specimen observed

31 Enlargement (x5) of proximal portion to show sicula, thecae and spines

32 Young rhabdosome

Ash hill quarry, Mt Moreno, Columbia co. N. Y.

PLATE 15

## Genus DIDYMOGRAPTUS McCoy

*See* pl. 13, 14

### Didymograptus bifidus Hall (sp.)

Page 689

1 Typical specimen. x2
2 Smaller rhabdosome
3 One of the largest and most complete rhabdosomes observed. x2
Graptolite bed 3 of the Deep kill section

### Didymograptus nanus Lapworth

Page 692

4 Mature rhabdosome
5 Proximal part of a rhabdosome. x5½
Graptolite bed 3 of the Deep kill section

### Didymograptus caduceus Salter *emend.* Ruedemann

Page 693

6, 7 Two specimens showing the prevailing expression of the form at the Deep kill. Natural size
Graptolite bed 2 of the Deep kill section

### Didymograptus caduceus Salter nanus mut. nov.

Page 698

8, 9 Two typical rhabdosomes. x2
Graptolite bed 6 of the Deep kill section

### Didymograptus forcipiformis sp. nov.

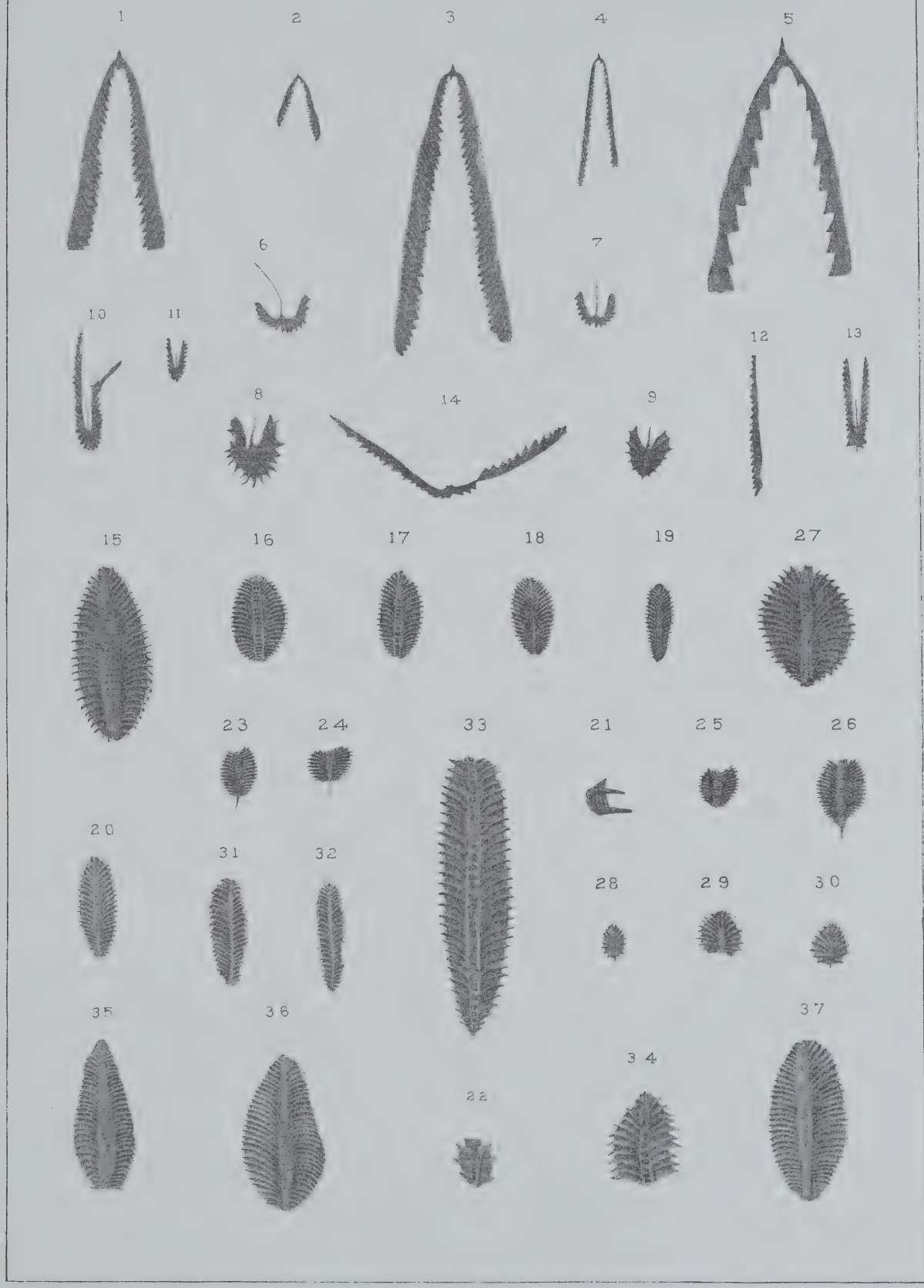
Page 699

10 Typical rhabdosome
11 Young rhabdosome
12 Branch of a long and thin branched rhabdosome
13 Specimen showing the large angle of divergence of the branches
Ash hill quarry, Mt Moreno, Columbia co. N. Y.

# GRAPTOLITES

Memoir 7. N.Y. State Museum

Plate 15




R.R.et G.S.B.del.

W.S. Barkentin.lith.

**Didymograptus incertus** sp. nov.

Page 700

14 Single specimen observed

Graptolite bed 7 of the Deep kill section

Genus PHYLLOGRAPTUS Hall

**Phyllograptus ilicifolius** Hall

Page 706

15 Specimen possessing the normal expression of the species. x2

16 Broad rhabdosome. The thecae are less curving in the original than in the figure

17, 18 Two forms with different positions of the broadest portions of the rhabdosomes

19, 20 Very narrow forms

21 Enlargement of the apertures of thecae. x5

22 Young rhabdosome showing the sicula. x5

The originals are from graptolite bed 2 of Deep kill section with the exception of that of figure 18, which is from graptolite bed 3.

**Phyllograptus anna** Hall

Page 714

23 Specimen with distinct sicular spine. The direction of the thecae on the left side has been incorrectly traced.

24, 25 Rhabdosomes showing the prevailing broadly truncate outline of the antisicular end. In figure 24 it is not quite correctly traced by the lithographer.

26 A relatively large and slender rhabdosome. The outline and the antisicular end have been incorrectly traced. The original is narrower and its margins less abruptly converging at the antisicular end.

Graptolite bed 5 of the Deep kill section

27 An enlargement (x2) to show more distinctly, the direction of the thecae The curvature of the thecae is more uniform on the right side than it is traced in the figure, and the mucros are lancet-shaped.

Top of graptolite bed 2 of the Deep kill section

28–30 Specimens showing the dwarfed and phylogerontic condition of the species at the disappearance of the genus in the horizon with Diplograptus dentatus (P. anna. mut. ultimus). Figure 28 in natural size, the original from the Ash hill quarry, Mt Moreno, Columbia co. N. Y.; figures 29 and 30, x2, the originals from graptolite bed 6 of the Deep kill section. In figure 29 the lithographer has left out the last thecae at the sicular end.

### Phyllograptus angustifolius

Page 711

31 Specimen showing the common expression of the species at the Deep kill section but incorrectly traced.

Graptolite bed 6 of the Deep kill section

32 A very narrow form

Graptolite bed 2 of the Deep kill section

33 Specimen from graptolite bed 5. x2¼. The thecal walls have been reproduced incorrectly by the lithographer. They are nearly straight in the original.

34 Fragment of young rhabdosome showing the growing end. x2

Graptolite bed 6 of the Deep kill section

### Phyllograptus typus Hall

Page 708

35–37 Specimens showing the variation in the outline of the rhabdosome

Graptolite bed 3 of the Deep kill section

PLATE 16

## Genus DIPLOGRAPTUS McCoy

*See* pl. 17

### Diplograptus laxus sp. nov.

Page 722

1 Typical rhabdosome

2, 3 Rhabdosomes with inflated nemacaulus

Ashhill quarry, Mt Moreno, Columbia co. N. Y.

4 Two specimens from graptolite bed 7 of the Deep kill section

5 Enlargement (x4½) to show the character of the thecae and the sicular end

6–8 Specimens which have a very lax or loose appearance. This is the prevailing appearance of the species at the Deep kill. x2

Graptolite bed 7 of the Deep kill section

9, 10 Natural size drawing and enlargement (x2) of a relatively long rhabdosome of more compact appearance

Graptolite bed 7 of the Deep kill section

### Diplograptus longicaudatus sp. nov.

Page 723

11 Single specimen observed. x2

Graptolite bed 7 of the Deep kill section

### Diplograptus inutilis Hall

Page 721

12 Nearly perfect rhabdosome

13 Enlargement (x2) of a fragment to show the character of the thecae

Graptolite bed 7 of the Deep kill section

## Genus CLIMACOGRAPTUS Hall

### Climacograptus pungens sp. nov.

Page 730

14 Rhabdosome (x4) showing typical climacograptid aspect and the apertural spines of the thecae

15 Relatively long specimen

16 Specimen of average size

17 Rhabdosome showing long filiform processes of the sicular end

Originals of figures 14 to 17 from Ash hill quarry, Mt Moreno, Columbia co. N. Y.

18 Specimen with the distinct thecal form of a Climacograptus. x2

Graptolite bed 7 of the Deep kill section

19 Rhabdosome with a different aspect of the thecae. x5

Ash hill quarry, Mt Moreno, Columbia co. N. Y.

20 Rhabdosome with long, stout sicular spines. x7

Graptolite bed 7 of the Deep kill section

### Climacograptus? (Cryptograptus) antennarius Hall

Page 731

21–23 Frontal views of rhabdosomes showing the long nemacaulus and long spines of the sicular end

24 Specimen showing the form of the thecae in the antisicular portion

25 Rhabdosomes showing the thecal aperture and character of the sicular end. x2

26 Rhabdosome showing apertural spines

Graptolite bed 7 of the Deep kill section

# GRAPTOLITES.

Memoir 7 N.Y. State Museum

Plate 16

R.R.et G.S.B. del.

W.S. Barkentin, lith.

Genus GLOSSOGRAPTUS Emmons, Lapworth *emend.*

**Glossograptus hystrix** sp. nov.

Page 724

27 Rhabdosome. x7

28–29 Specimens showing the multispinous character of the rhabdosome. x2

Graptolite bed 7 of the Deep kill section

**Glossograptus echinatus** sp. nov.

Page 725

30, 31 Small rhabdosomes showing the distribution of the spines

32 Nearly perfect rhabdosome

Graptolite bed 7 of the Deep kill section

Genus RETIOGRAPTUS Hall

**Retiograptus tentaculatus** Hall

Page 733

33, 34 Rhabdosomes showing the prevalent expression of the form in the Deep kill beds. x2

35 Specimen showing the extrathecal meshes. x2

Graptolite bed 7 of the Deep kill section

PLATE 17

## Genus TRIGONOGRAPTUS Nicholson

### Trigonograptus ensiformis Hall (sp.)

Page 727

1 Very young rhabdosome

2 A more advanced growth stage

Ash hill quarry, Mt Moreno, Columbia co. N. Y.

3 Largest specimen observed

4, 5 Fragments of rhabdosomes showing the thecal walls

6 Rhabdosome which shows the thecal apertures

7 Fragment of another rhabdosome which shows the thecal apertures

8 Nearly complete rhabdosome in which the process of the sicular end is retained

9 Rhabdosome in which the direction of the apertural margins in relation to the axis of the thecae is shown. x2

Graptolite bed 7 of the Deep kill section

## Genus DIPLOGRAPTUS McCoy

*See* pl. 16

### Diplograptus dentatus Brongniart (sp.)

Page 719

10, 11 Rhabdosomes of typical appearance and dimensions

Ash hill quarry, Mt Moreno, Columbia co. N. Y.

12 Frontal aspect of a rhabdosome

Graptolite bed 7 of the Deep kill section

13 A young rhabdosome retaining the long sicular spine

Ash hill quarry, Mt Moreno, Columbia co. N. Y.

## Genus CARYOCARIS Salter

### Caryocaris cf. oblongus Gurley

Page 738

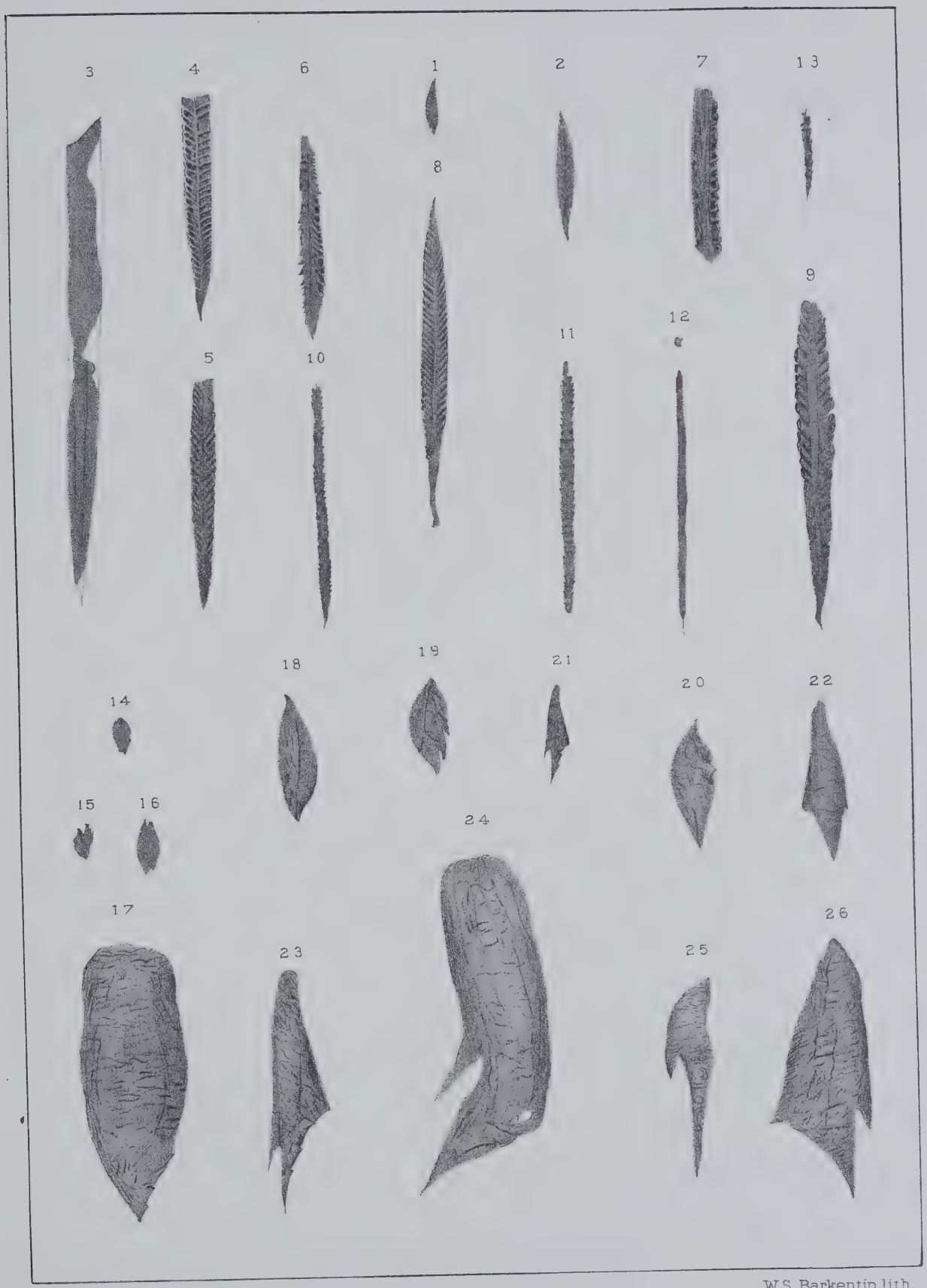
14–16 Three of the most common aspects of the organism

Lower Cham plainic beds at the Mettanee river, east of North Granville, Washington co. N. Y.

# GRAPTOLITES

Memoir 7 N.Y. State Museum

Plate 17




R.R.et G.S.B. del.

W.S. Barkentin, lith.

**Caryocaris** cf. **curvilineatus** Gurley

Page 738

17 Prevailing aspect of the bodies at the Deep kill section, referred to this species. x6½

Graptolite bed 1 of the Deep kill section

Genus DAWSONIA Nicholson

**Dawsonia tridens** Gurley

Page 741

18 Specimen showing incisions suggestive of thecae and a longitudinal axis. x7

19 A similar specimen with more distinct denticles. x6

Graptolite bed 2 of the Deep kill section

20 A specimen showing two thecoid tubes. x7

Graptolite bed 1 of the Deep kill section

**Dawsonia monodon** Gurley

Page 741

21 Complete specimen showing a long median and two lateral appendages. x2

22 A smaller specimen with less developed lateral appendages. x6½

23 A further enlargement of the original of figure 21 (x6½) to show more distinctly the thecal tubes of the middle appendages

24 A specimen with strongly developed narrow, lateral appendages. x8

Graptolite bed 1 of the Deep kill section

25 Frontal view of a middle appendage showing four apertures. x7

Graptolite bed 3 of the Deep kill section

26 A specimen with broad median and short lateral appendages. x6½

Graptolite bed 1 of the Deep kill section

# INDEX

Page numbers referring to descriptions of fossils are printed in black face type.


**Acrotreta**, 739.
Actinozoa, 532.
Aglaophenia, 588.
Allman, G. J., cited, 461, 474, 477, 524, 544, 574, 575.
America, graptolite beds, 488.
Ami, H. M., cited, 463, 471, 472, 490, 580, 585, 589, 621, 623, 633, 651, 656, 660, 669, 672, 690, 710, 713, 715, 739.
Amphigraptus, 544, 571, 701.
Anthozoa, 577.
Antisicular end of rhabdosome, 484.
Antisiculaseite, 484.
Apertural margin, 486.
Apertural spine, 486.
Aperture, 486.
Ardennes, graptolite fauna, *following* p.503.
Arenig, graptolite fauna, 505, 507, 651, 687, *following* p.503; lower, 580, 587, 610, 669, 729; middle, 580, 585, 610, 673, 675; upper, 675, 690, 693, 720.
Arkansas, graptolite fauna, 505, 507, 656, 715, 720, 729, 731, *following* p.503.
Arme, 484.
Australia, graptolite fauna, 471, 488, 503, 505, 507, 621, 633, 651, 660, 743–46, *following* p.503. *See also* Victoria.
Axonolipa, 487, 488, 514, 515, 516, 518, 519, 522, 523, 526, 527, 529, 535, 536, 537, 539, 546, 547, 548, 570, 571, 573, 577, 612–718; synoptic table of range of genera, 508; connection with Axonophora, 550.
Axonophora, 483, 487, 488, 499, 514, 515, 518, 525, 526, 528, 529, 530, 535, 536, 539, 546, 547, 548, 551, 552, 553, 570, 571, 572, 574, 575, 718–34; synoptic table of range of genera, 508; connection with Axonolipa, 550.
Azygograptus, 536, 568, 624.
  lapworthi, 555.
  suecicus, 555.

**Ballantrae**, Scotland, graptolite fauna, 646, 669, 687.
Barrande, J., cited, 459, 467, 468, 469, 472, 479, 484.
Barrois, C., cited, 464, 471, 495, 647, 657, 673, 691.
Basal cyst, 488.
Beck, cited, 467.
Beekmantown beds, 585, 611, 715, 737, 738, 740, *following* p.503.
Belgium, graptolite fauna, 505, 507, 602, 636, 637, *following* p.503; Dictyonema zone, 492; Tetragraptus zone, 495. *See also* Huy-Statte.
Bellerophon oehlerti, 691.
Bendigo series, 744, 746.
Billings, cited, 470, 495, 589, 651, 656, 710, *following* p.503.
Bohemia, graptolite fauna, 467, 469, 470, 471, 477, 489, 502, 505, 507, 660, 691, *following* p.503; St Anne zone, 498.
Bornholm, graptolite fauna, 602, *following* p.503; Dictyonema zone, 492.

Boutoury, graptolite fauna, 657, 673, 691.
Brachiopods of the graptolite shales, 739.
Branches, 484; terms for characteristic positions, 485.
British Columbia, graptolite fauna, *following* p.503.
Brittany, graptolites, 471.
Brögger, W. C., cited, 462, 471, 492, 592, 593, 605, 636, 647, 651, 657, 660, 669, 676, 687, 691, 693, 710, 713.
Bromell, M. v., cited, 459, 466.
Brongniart, A., cited, 459, 466.
Bryograptus, 492, 495, 508, 531, 533, 537, 549, 554, 555, 562, 563, 566, 567, 568, 571, 573, 616, **638–39**, 743, 745; graptolites derived from, 555.
*sp.*, 562.
*sp. nov.*, 639.
callavei, 555, 640.
divergens, 640.
fruticosus, *see* Tetragraptus (Bryograptus?) fruticosus.
kjerulfi, 638, 640, 641, 642.
lapworthi *sp. nov.*, 504–5, 557, 558, 560, 561, 573, 638, **639–41**, 682, 683, 684.
explanation of plate, 756.
figure, 639.
lentus, 614.
? multiramosus, 600.
patens, 614.
pusillus *sp. nov.*, 504–5, 573, 639, **641–42**.
explanation of plate, 755.
ramosus, 640.
*var.* cumbrensis, 555, 556, 559, 639.

Cabrières, graptolite fauna, 505, 507, 647, *following* p.503.
Callograptus, 469, 495, 503, 508, 537, 571, 572, **583–84**, 610; phylogenetic relations of genera, 553.
*cf.* diffusus, 504–5, 572, **586–87**.
explanation of plate, 754.
figure, 587.
elegans, 585, 586.
radicans, 586.
salteri, 504–5, 572, **584–86**.
explanation of plate, 753.
figures, 585.
Calycles, 485.
Canada, graptolite fauna, 468, 472, 492, 503, 585, 589, 601, 602, 633, 673, 678, 739; graptolite zones, correlation table, *following* p.503; Tetragraptus zone, 495. *See also* Point Levis; St Anne beds.
Canal commun, 486.
Canal in the Graptoloidea, 486.
Caradoc shales, *following* p.503.
Carruthers, W., cited, 460, 470, 477, 574.
Caryocaris, 495, 508, 574, **735–38**.
*cf.* curvilineatus, 506–7, 574, 738.
explanation of plate, 783.
oblongus, 738.
explanation of plate, 782.
figure, 738.
wrightii, 735, 736, 737, 738.
figure, 737.
Castlemaine series, 744, 746.
Cells, 485.
Cellules, 485.
Central disk, 487.
Cephalograptus, 514.
Ceratopyge limestone, 495.
Champlainic shales, upper, 722.
Chaudière river, graptolite fauna, 715.
Chazy limestone, *following* p.503.

Christiania, graptolite fauna, 505, 507, 602, 636, 638, 647, 657, 660, 669, 691, 695, 710, 713, *following* p.503.
Cincinnati shales, lower, *following* p.503.
Cladophora, 544.
Clarke, John M., acknowledgments to, 457; cited, 480.
Classification of graptolites, 543–74.
Clathrograptus, 518, 545, 547.
Cleland, H. F., mentioned, 585.
Clematograptus, 612, 613, 614.
implicatus, 613.
Climacograptidae, 489, 517, 518, 538, 539, 572, 574, 729–34.
Climacograptidi, 546.
Climacograptus, 474, 476, 478, 483, 498, 499, 508, 538, 544–45, 546, 550, 551, 570, 574, 579, 718, **729**, 731, 744.
*sp.*, 744.
*sp. nov.*, 730.
? (Cryptograptus) antennarius, 506–7, 574, 587, 608, 610, 725, 729, **731–32**, *following* p.503.
explanation of plate, 780.
zone, 498–500.
bicornis, 514, 543.
caudatus, 491, *following* p.503.
kuckersianus, 538.
pungens *sp. nov.*, 499, 500, 506–7, 574, 729, **730**.
explanation of plate, 780.
scharenbergi, 730.
styloideus, *following* p.503.
vasae, *following* p.503.
wilsoni, *following* p.503.
Clinton formation, species from, 467.
Clonograptus, 492, 494, 496, 531, 537, 544, 545, 549, 555, 556, 562, 563, 566, 567, 568, 571, 573, 612, 614, 617, 618, 620, 745; graptolites derived from, 556.
*sp.*, 656, 744.
(Staurograptus) dichotomus, 562, 563.
*cf.* flexilis, 496, 504–5, 573, 606, **618**, 743, 745.
milesi, 617, 618.
proximatus, 492, 502, 601, 603, 613, 614.
rigidus, 496, 589, 743, 745.
*var.* tenellus, 743.
tenellus, 502.
thureaui, *see* Dichograptus (Clonograptus, Goniograptus) thureaui.
Clonograptus bed, 496.
Clonograptus subzone, *following* p.503.
Cluysenaar, cited, 636; mentioned, 710.
Cnidaria, 521.
Coenograptidae, 564, 571, 572, 573, 701–3.
Coenograptus, 497, 509, 537, 544, 564, 566, 567, 568, 571, 645, 702, 717.
gracilis, 564, 565, 571, 666, 701, 703, 717, *following* p.503.
Coenosarcal canal, 486.
Colonie, 483.
Columbia county, species from, 467.
Common canal, 486.
Connecting canal, 484, 536.
Conularia trentonensis, 491.
Conularias, 518.
Correlation table of zones in the Cambric and Champlainic of the slate belt of New York, *following* p.503.
Corynoides curtus, *following* p.503.
Cowhead, Newfoundland, graptolite fauna, 495, 651, 656, 710.

Crossing canal, 484, 536, 550.
Cryptograptus, 498, 731, 732.
antennarius, *see* Climacograptus? (Cryptograptus) antennarius.
hopkinsoni, 732.
tricornis, 491, 732, *following* p.503.
Ctenograptus, 537.
Cumings, E. R., cited, 526, 534.
Cups, 485.
Cysts, 521.

Dalarne, Sweden, graptolite fauna, 505, 507, 636, 681.
Dale, T. N., cited, 496; mentioned, 601; collections by, 618, 646.
Dalecarlia, graptolite fauna, 647, 657.
Dames, W., cited, 461, 592, 603.
Darriwill series, 744.
Dawson, cited, 492, 601; mentioned, 608.
Dawsonia, 495, 508, 521, 574, **735–40.**
acuminata, 738, 739, 741.
campanulata, 739.
monodon, 506–7, 574, 737, 740, **741–42.**
explanation of plate, 783.
figure, 742.
rotunda, 739.
tenuistriata, 739.
tridens, 506–7, 574, 740, **741.**
explanation of plate, 783.
Dease river, graptolite fauna, *following* p.503.
Deep kill, Goniograptus from, 471; graptolite fauna, 491, 494, 498, 503, 504, 506, 508, 540, 542, 550, 555, 560, 579, 581, 583, 584, 589, 590, 591, 607, 608, 609, 610, 612, 620, 621, 623, 625, 629, 633, 636, 637, 638, 639, 640, 646, 648, 651, 657, 659, 661, 662, 664, 666, 670, 672, 673, 675, 678, 682, 690, 694, 705, 708, 711, 712, 715, 718, 719, 720, 721, 722, 723, 726, 728, 729, 730, 731, 734, 739, 740, 741, 742, 745, *following* p.503.
Defreestville, graptolite fauna, 606, 753.
Dendrograptidae, 571, 572, 578–612; phylogeny, 553.
Dendrograptidi, 546, 548.
Dendrograptus, 469, 477, 478, 495, 500, 503, 508, 536, 537, 540, 544, 546, 567, 571, 572, **578–79**, 584, 587; phylogenetic relations of genera, 553.
*sp.*, 499, 744.
*sp. nov.*, 581, 582.
(Callograptus?) diffusus, 586.
divergens, 580.
erectus, 581.
flexuosus, 504–5, 572, **579–80**, 583.
explanation of plate, 754.
fluitans *sp. nov.*, 504–5, 572, **582-83.**
explanation of plate, 754.
fruticosus, 580.
*cf.* gracilis, 579.
hallianus, 578, 582.
serpens, 581.
succulentus *sp. nov.*, 504–5, 572, 578, 580, **581–82.**
explanation of plate, 754.
figures, 581, 582.
Dendroid, 522.
Dendroidea, 477, 483, 488, 495, 497, 500, 503, 509, 513, 514, 515, 521, 522, 523, 526, 529, 535, 536, 537, 539, 544, 546, 567, 570, 571, 572, 578–612; synoptic table of range of genera, 508; relation to Graptoloidea, 548–49; phylogenetic relations of genera, 553.
Denticles, 485.
Descriptions of graptolites, 578–734.

Desmograptus, 508, 571, 573, 599, **609**; phylogenetic relations of genera, 553.
cancellatus, 504–5, 573, 609, **610–11**.
explanation of plate, 752.
figure, 610.
devonicus, 599.
intricatus *sp. nov.*, 504–5, 573, 599, 609, **611–12**.
explanation of plate, 752.
figures, 609, 611, 612.
macrodictyum, 610, 611.
Dicellocephalus fauna, 493.
Dicellograptus, 474, 544, 546, 552, 553, 666.
anceps, *following* p.503.
complanatus, *following* p.503.
divaricatus *var.* rigida, 514.
moffatensis, 552.
Dicellograptus zone, lower, *following* p.503; upper, *following* p.503.
Dichograpsus aranea, 634, 637.
octobrachiatus, 635.
sedgewickii, 637.
Dichograptid, 522; figure showing sicula, 520.
Dichograptidae, 468, 475, 476, 478, 483, 486, 487, 489, 494, 497, 499, 515, 517, 525, 527, 528, 529, 530, 531, 532, 535, 536, 538, 544, 545, 546, 547, 548, 549, 550, 551, 554, 555, 563, 564, 567, 571, 573, 604, 612–701; phylogeny of, 553, 554; supposed causes of evolution, 542, 567–70.
Dichograptidi, 546.
Dichograptus, 470, 473, 508, 516, 531, 535, 537, 544, 554, 563, 566, 567, 568, 571, 573, 620, 630, **634**, 637, *following* p.503.
*sp.* figure 541.
hexabrachiatus, 637.
Dichograptus kjerulfi, 631, 633.
logani, 631, 632.
octobrachiatus, 494, 495, 497, 504–5, 542, 556, 573, 585, 630, 633, **634–37**, 669, 683, 686, 744, 746.
explanation of plates, 762, 764.
et hexabrachiatus, 635.
octonarius, 556, 634, 744.
separatus, 559, 634.
(Clonograptus, Goniograptus) thureaui, 621.
Dichograptus beds, 495, 636.
Dichograptus zone, *following* p.503.
Dichotomous branching, 485.
Dicranograptidae, 544.
Dicranograptus, 474, 544, 546, 553.
clingani, *following* p.503.
Dictyograptus, 599.
*n. sp.*, 608.
(Desmograptus) cancellatus, 610, 611.
flabelliformis, 600.
Dictyonema, 467, 469, 476, 477, 478, 495, 503, 508, 509, 513, 527, 535, 536, 537, 544, 546, 549, 556, 563, 571, 573, 578, 579, 584, **591–99**, 604, 743; mode of life, 593; phylogenetic relations of genera, 553.
(Desmograptus) *sp. nov.*, 606, 607, 611.
blairi, 488.
(Desmograptus) cancellatum, 610.
cavernosum, 594, 596, 598, 604, 607.
figures, 595, 597.
cervicorne, 607.
figure, 592.
delicatulum, 607, 608.
flabelliforme, 478, 479, 504–5, 515, 521, 526, 527, 535, 549, 563, 567, 573, 586, 592, 593, 594, 595, 597, 598, **599–606**, 614, 615, *following* p.503.

Dictyonema flabelliforme, explanation of plate, 748–49.
figures, 601, 602.
*var.* confertum, 605.
explanation of plate, 749.
*mut.* norvegicum, 605.
zone, 491, 492–93, 501–2, 508.
furciferum *sp. nov.*, 504–5, 573, **606–7.**
explanation of plate, 752.
figure, 607.
graptolithinum, 600.
hisingeri, 599.
irregularis, 496.
murrayi, 496, 504–5, 573, **606,** 656.
explanation of plate, 753.
norvegicum, 600, 605.
*var.* acadicum, 605.
peltatum, 549, 607.
perexile, 608.
rarum, figures, 593, 594.
rectilineatum *sp. nov.*, 504–5, 573, **607–9,** 612.
explanation of plate, 752.
figure, 608.
robusta, 496.
sadewitzense, 600.
sociale, 600.
tuberosum, 599.
Dictyonema zone, 490.
Didymograpsus bryonoides, *see* Graptolites (Didymograpsus) bryonoides.
caduceus, 655, 658, 693.
extensus, *see* Graptolites (Didymograpsus) extensus.
fruticosus, *see* Graptolites (Didymograpsus) fruticosus.
geminus, 692.
Didymograpsus logani, *see* Graptolites (Didymograpsus) logani.
nitidus, 671.
octobrachiatus, *see* Graptolites (Didymograpsus) octobrachiatus.
quadribrachiatus, *see* Graptolites (Didymograpsus) quadribrachiatus.
Didymograptidae, 530, 546, 550, 718–29.
Didymograptini, 546.
Didymograptus, 474, 476, 478, 494, 495, 497, 508, 509, 516, 531, 535, 537, 544, 549, 552, 554, 555, 560, 562, 563, 566, 567, 568, 571, 573, 610, 660, **666–68,** 695, 743, 744.
figure, 485.
(Leptograptus) *sp.*, 680.
*sp. nov.*, 679, 682, 700.
acutidens, 506–7, 560, 573, 667, **683–84,** 685.
explanation of plate, 773.
figures, 683, 684.
affinis, 555, 562, 667, 682, 683, 688.
arcuatus, 556.
balticus, 679.
bifidus, 497, 498, 499, 506–7, 536, 555, 557, 559, 573, 579, 586, 590, 591, 608, 609, 621, 623, 626, 627, 629, 636, 651, 652, 654, 657, 659, 660, 665, 666, 667, 670, 675, 678, 680, ?683, 688, **689–92,** 693, 694, 703, 707, 710, 713, 715, 744, 745, 746, *following* p.503.
explanation of plate, 776.
figure, 691.
zone, 496–98, 504, 506, 508, 653, 656, 746.
(Isograptus) caduceus, 506–7, 550, 573, 658, 660, 662, 668, **693–98,** 699, 700, 744.
explanation of plate, 776.

Didymograptus caduceus nanus *mut. nov.*, 506–7, 668, **698**, 700.
explanation of plate, 776.
figure, 698.
(gibberulus) 497, 550, 551, 555, 562, 570, 653, 654, 677, 693, 694, 696, 697, 698, 699.
constrictus, 585, 668, 670, 671.
cuspidatus *sp. nov.*, 499, 500, 506–7, 560, 573, 667, **684–85**.
explanation of plate, 773.
figures, 684, 685.
decens, 678, 679, 744.
(indentus) dentatus, 655.
ellesi *sp. nov.*, 506, 557, 558, 573, 667, **682–83**.
explanation of plate, 775.
figures, 682.
extensus, 504–5, 516, 548, 556, 557, 562, 569, 573, 608, 648, 667, **668–71**, 672, 673, 678.
explanation of plates, 773, 774.
figures, 669, 670.
filiformis, 499, 500, 506–7, 561, 562, 565, 573, 667, **686–87**.
explanation of plate, 774.
forcipiformis *sp. nov.*, 499, 506–7, 562, 573, 668, **699–700**.
explanation of plate, 776.
figure, 699.
fractus, 652.
? fruticosus, 649.
furcillatus, 555, 559, 608.
geminus, *following* p.503.
(Isograptus) gibberulus, 669, 694.
*var.* nanus *var. nov.*, 694.
gracilis, 499, 500, 506–7, 533, 555, 558, 561, 562, 565, 573, 667, **679–81**, 682, 744.
Didymograptus gracilis, explanation of plate, 775.
figure, 533.
incertus *sp. nov.*, 506–7, 552, 573, 668, **700–1**.
explanation of plate, 777.
figure, 700.
indentus, 555, 559, 667, 693.
*var.* nanus, 692.
murchisoni, 637, 667, 690, 744.
nanus, 497, 506–7, 573, 667, 680, 682, **692–93**.
explanation of plate, 776.
nicholsoni, 555, 557, 558, 562, 675.
*var.* planus, 506–7, 573, 667, **685–86**, 688.
explanation of plate, 773.
figures, 685, 686.
nitidus, 504–5, 530, 557, 562, 569, 573, 663, 667, **671–74**, 675, 676, 677, 679.
explanation of plates, 772, 774.
figures, 672, 673.
*var.* grandis, 674.
explanation of plate, 772.
patulus, 504–5, 516, 530, 535, 556, 557, 569, 573, 667, 671, 673–74, **674–77**.
explanation of plates, 772, 774.
figures, 675, 676, 677.
pennatulus, 608.
sagittarius, 678.
similis, 497, 506–7, 557, 573, 652, 667, **677–79**, 688.
explanation of plate, 775.
figures, 678.
spinosus *sp. nov.*, 499, 500, 506–7, 558, 573, 667, **688–89**.
explanation of plate, 775.
figures, 689.

Didymograptus suecicus, 678, 679.
(Goniograptus) thureaui, 621.
törnquisti *sp. nov.*, 506, 530, 573, 667, **688.**
explanation of plate, 772.
Dimorphograptus, 475, 478, 526, 547.
Diplograpsus, 470.
antennarius, 731.
folium, 710.
Diplograptidae, 489, 499, 514, 517, 518, 538, 539, 544, 545, 547, 550, 551, 570, 571, 572, 574, 718–29.
Diplograptidi, 546.
Diplograptus, 468, 474, 476, 478, 479, 483, 486, 488, 499, 508, 510, 511, 513, 518, 519, 521, 522, 525, 529, 538, 539, 540, 542, 545, 547, 550, 551, 552, 570, 572, 574, 577, 579, **718–19,** 731.
*sp.*, 744.
figures, 520, 529.
*sp. nov.*, 722, *following* p.503.
amplexicaulis, 491, *following* p.503.
angustifolius, *following* p.503.
appendiculatus, 535, 723.
cancellatus, 612.
dentatus, 499, 500, 503, 506–7, 539, 550, 552, 557, 574, 580, 581, 586, 587, 589, 608, 609, 610, 611, 612, 626, 632, 636, 637, 646, 664, 665, 672, 678, 680, 685, 687, 689, 690, 693, 695, 698, 699, 700, 712, 713, 715, 716, 718, **719–21,** 723, 725, 726, 728–29, 730, 731, 732, 734, 745, 746, 778, *following* p.503.
explanation of plate, 782.
figure, 720.
zone, 498–500, 504, 506, 508, 722.
foliaceus, 478, 479, 525, 526, 528, 542, *following* p.503.
figures, 528.
Diplograptus inutilis, 506–7, 574, 718, **721.**
explanation of plate, 779.
laxus *sp. nov.*, 499, 500, 506–7, **519, 574,** 718, **722–23.**
explanation of plate, 779.
longicaudatus *sp. nov.*, **506–7, 574, 718, 723.**
explanation of plate, 779.
physophora, 514, 519.
pristiniformis, 719.
(dentatus), 637.
pristis, 542, *following* p.503.
pusillus, *following* p.503.
putillus, 722.
quadrimucronatus, *following* p.503.
sertularioideus, 723.
teretiusculus, 723.
vesiculosus, 519, 723.
whitfieldi, 477, 520.
Diprion, 718.
Diprionidae, 475, 544, 545.
Diprionidian, 484.
Discograptus schmidti, 596.
Disk, central, 487.
Dorsal edge of canal, 486.
Dorsal wall, 486.
Dumfriesshire, black shales of, 470.
Dun, W. S., cited, 743.

Ellergill beds, 633, 720, 725, 726, 729, 730, 734, *following* p.503. *See also* Skiddaw slates.
Elles, G. L., cited, 459, 465, 471, 478, 484, 485, 495, 502, 525, 535, 536, 549, 550, 554, 555, 556, 558, 563, 616, 617, 618, 631, 633, 634, 637, 638, 639, 640, 641, 643, 644, 648, 653, 661, 667, 673, 675, 676, 687, 690, 695, 696, 699, 706, 708, 709, 711, 713, 715, 717,

720, 724, 726, 727, 729, 730, 731, 732, *following* p.503; investigations, 553; mentioned, 567.
Emmons, E., cited, 459, 460, 467, 612, 716, 717; mentioned, 615.
England, graptolite fauna, 469, 490, 505, 507, 512, 633, 636, 660; Dictyonema zone, 492; Tetragraptus zone, 495. *See also* Ellergill beds; Lake district.
Esthland, Dictyonema zone, 492.
Esthonia, graptolite fauna, 602, *following* p.503.
Etagraptus, **644–45.**
lentus, *see* Tetragraptus (Etagraptus) lentus.
Etheridge, R. jr, cited, 461, 471, 495, 660, 673, 695, 697, 735, 736.
Eudendrium, 521.
ramosum, 524.
figures, 523.
Europe, graptolite fauna, 502, 601, 602; Tetragraptus zone, 495.
Explanation of plates, 747–53.

**Fairhaven** (Vt.), Dictyonema zone, 493; graptolite fauna, 601.
Fenestella flabelliformis, 599.
Fichtelgebirge, graptolite shales, 471.
France, graptolite fauna, 471, 488, 489, 502, 505, 507, *following* p.503; Tetragraptus zone, 495; St Anne zone, 498. *See also* Boutoury.
Frech, F., cited, 459, 465, 484, 488, 501, 503, 514, 515, 521, 536, 542, 545, 546, 547, 548, 570, 571, 572, 577, 588, 592, 617, 620, 630, 669, 693, 695, 718, 723, 724, 732, 733, 734, 746.
Frond, 483.
Fucoides dentatus, 719.
serra, 655.
"Funicle," 473, 486.
"Fuss," 473, 484.

**Gaspé**, graptolite fauna, *following* p.503.
Geinitz, H. B., cited, 459, 460, 467, 468, 470, 509.
Gembloux, shale of, *following* p.503.
Gemeinsamer Canal, 486.
Germany, graptolites from, 471.
Girvan, graptolite shales, 512.
Glenkiln shales, *following* p.503.
Glossograpsus, 467.
Glossograptidae, 545.
Glossograptus, 499, 508, 539, 545, 547, 550, 572, 574, 718, **724**, 744, *following* p.503.
*sp. nov.*, 724.
armatus, 725, 726.
echinatus *sp. nov.*, 506–7, 574, **725–26.**
explanation of plate, 781.
figure, 726.
fimbriatus, 725, 726, 734.
hincksii, 725, 726.
hystrix *sp. nov.*, 499, 506–7, 574, **724–25**, 726.
explanation of plate, 781.
figure, 725.
Goniograptus, 471, 494, 503, 508, 528, 532, 533, 534, 536, 542, 566, 567, 571, 573, **620–21.**
*sp. nov.*, 625, 627.
geometricus *sp. nov.*, 497, 504–5, 565, 573, **627–30**, 652, 654, 665, 666, 680, 688.
explanation of plate, 760-61.
figures, 628, 629.

Goniograptus macer, 744.
perflexilis *sp. nov.*, 500, 504–5, 559, 561, 565, 573, **625–27**, 644, 662–63, 681.
explanation of plate, 759, 760.
figures, 625, 626, 627.
*mut.*, 499.
thureaui, 478, 479, 503, 504–5, 526, 527, 531, 569, 573, **621–24**, 626, 627, 631, 638, 652, 661, 744.
figures, 622.
*var.* postremus, 623.
*var. nov.*, explanation of plate, 758-59.
*var.* selwyni, 621.
Goniograptus subzone, *following* p.503.
Gorgonia flabelliformis, 599.
Gothland, graptolite fauna, 592, 597, 602, 607.
Gothograptus, 518, 547, 733.
Grabau, A.W., discovery of Phyllograptus, 499.
Granville, graptolite fauna, 595, 601; Dictyonema zone, 493.
Graptolite shales, 479, 695.
Graptolites, animal nature, 467; central or basal portions of colonies, 473; classification and phylogeny, 543-74; derived from Bryograptus, 555; derived from Clonograptus, 556; descriptions, 578–734; some general facts of distribution, 500–3; Hall's views, 468; histology and chemical composition of the periderm, 539–43; history of the study of, 466–78; similarity to hydrozoans, 467; internal structure, 472; methods of illustration, 481; methods of investigation and illustration, 479-82; mode of existence, 469, 478, 509–19; mode of reproduction and development, 477–78; mode of reproduction and ontogeny, 519–34; mode of suspension, 515; phylogeny of genera and species, 478, 553–67; phylogeny of orders, 548–53; range and geographic distribution, 488–508; stratigraphic relations, 469; structure and morphology, 534–39; taxonomic relations, 574–77; term, 466; terminology, 482–88; vegetable origin, 466.
Graptolites (Didymograpsus) bryonoides, 655.
caduceus, 658, 693.
extensus, 668.
fruticosus, 649.
gracilis, 679.
logani, 631.
octobrachiatus, 635.
quadribrachiatus, 645.
thureaui, 621.
Graptolithus, 466, 477, 574.
bifidus, 689.
bigsbyi, 658.
bryonoides, 647, 655.
caduceus, 697.
constrictus, 668.
divergens, 701.
extensus, 668.
flexilis, 618.
fruticosus, 649.
logani, 630, 631.
milesi, 544, 617.
multifasciatus, 544.
nitidus, 671.
octobrachiatus, 634, 635.
patulus, 674.
pristiniformis, 719.
quadribrachiatus, 645.
ramosus, 473.
richardsoni, 544.
similis, 660.

Graptolithus tentaculatus, 733.
vagans, 544.
Graptolitidae, 544, 545, 570.
Graptoloidea, 487, 488, 503, 509, 514, 515, 522, 526, 536, 537, 539, 546, 571, 573, 574, 604, 612–734; canal in, 486; relation to Dendroidea, 548-49.
Graptopora socialis, 599.
Graptothecae, 485.
Great Britain, graptolite fauna, 470, 471, 472, 474, 488, 489, 490, 498, 512, 646, 673, 690, 710, 713; graptolite zones, correlation table, *following* p. 503; Dictyonema zone, 492-93. *See also* Lake district; Scotland; Wales.
Greenfield limestone, 493.
Grenarne, 484.
Gros Maule, Canada, graptolite fauna, 585.
Gümbel, C. W., cited, 462, 476, 477, 480, 539–40, 543.
Gürich, G., cited, 464, 477, 480, 511, 515, 540.
Gurley, R. R., cited, 464, 465, 472, 488, 490, 495, 498, 580, 585, 589, 590, 599, 608, 611, 633, 636, 651, 656, 660, 672, 675, 690, 710, 715, 717, 720, 721, 728, 731, 735, 737, 738, 740, 741, 745, *following* p.503.

Haftorgan, 484.
Hall, James, cited, 457, 459, 460, 466, 467, 468, 469, 471, 473, 477, 479, 486, 487, 490, 496, 497, 509, 517, 519, 520, 527, 544, 574, 582, 583, 585, 587, 588, 589, 590, 591, 593, 613, 629, 630, 632, 634, 636, 637, 647, 648, 651, 656, 657, 659, 660, 661, 670, 671, 672, 675, 676, 678, 690, 692, 703, 705, 706, 709, 710, 715, 716, 717, 721, 724, 728, 729, 731, 732, 734; mentioned, 646, 669.
Hall, T. S., cited, 464, 498, 743, 744, 745, 746.
Hamilton group, Dictyonemas in, 509.
Harkness, cited, 470.
Hartfell shales, *following* p.503.
Hartz, graptolites, 474.
Haut, 486.
Hector, James, cited, 743.
Herrmann, M. O., cited, 463, 475, 509, 617, 630, 636, 673, 676, 691.
Hicks, cited, 736.
Hillsdale, graptolite fauna, 601, 615, 617.
Hisinger, W., cited, 459.
Holm, G., specimens drawn by, 481; cited, 462, 463, 464, 476, 478, 480, 484, 485, 495, 520, 521, 523, 525, 526, 534, 536, 547, 563, 584, 592, 597, 598, 643, 660, 661, 665, 695, 705, 706; mentioned, 713.
Holograptus, 537, 618.
richardsoni, 619, 620.
Hopkinson, J., cited, 461, 462, 470, 474, 475, 503, 544, 548, 580, 582, 583, 585, 586, 587, 588, 599, 609, 657, 666, 720, 729.
Hudson, *see* Mt Moreno.
Hudson river shales, species from, 467; investigation of, 472; position, 490; faunal zones, 490, 491.
Hunneberg, fauna, 669.
Huxley, cited, 477.
Huy-Statte, Belgium, graptolite fauna, 710, *following* p.503.
Hyatt, cited, 534, 550.
Hydrocaulus, 487.
Hydroidea, 474, 518, 521, 522, 525, 526, 576.
Hydrorhabd, 484.
Hydrosome, 483.
Hydrothecae, 485.
Hydrozoa, 477, 514, 532, 577.

Initial point, 484.
Inocaulis, 477, 478, 537.
Ireland, Dictyonema zone, 492; graptolite fauna, 602. *See also* Kiltrea.
Isograptus, 695, 696.
caduceus, *see* Didymograptus (Isograptus) caduceus.
gibberulus, *see* Didymograptus (Isograptus) gibberulus.

Jackson, R. T., cited, 532, 624.
Jaekel, O., cited, 463, 475, 510, 511, 515.
Jones, cited, 735, 736, 737.

Kerforne, cited, 471.
Kicking Horse pass, graptolite fauna, *following* p.503.
Kiltrea, Ireland, graptolite fauna, 675.
Krekling, Norway, graptolite fauna, 660, 676, 687, 693.

Lake district, graptolite fauna, 651, 653, 654, 657, 669, 672, 686, 691, 693, 710, 715.
Lake St John, Canada, graptolites from, 468.
Lancefield series, 743, 745.
Languedoc, graptolite fauna, 647.
Lansingburg, graptolite fauna, *following* p.503.
Lapworth, C., microscope constructed by, 481; cited, 461, 462, 463, 470, 472, 473, 474, 475, 476, 478, 479, 484, 485, 487, 488, 489, 490, 492, 497, 498, 503, 511–12, 512–13, 514, 515, 520, 526, 544, 545, 546, 547, 549, 568, 570, 571, 580, 582, 583, 585, 587, 595, 596, 597, 602, 608, 613, 620, 634, 648, 657, 669, 670, 672, 673, 675, 676, 690, 693, 695, 696, 704, 715, 717, 718, 720, 729, 731, 732, 737, 739, *following* p.503.
Lapworth, H., cited, 465, 471.
Lasiograptus, 518, 521, 541, 543, 545, 547, 734, 744.
Lateral branching, 485.
Lateral walls, 486.
Lecrenier, A., cited, 463, 636; mentioned, 710.
Leptograptidae, 546, 571, 572.
Leptograptus, 544, 571, 743.
flaccidus, *following* p.503.
Lindström, Prof., cited, 511.
Linea, 487.
Lingula flags, 505, 507, *following* p.503.
Linnarsson, G., cited, 462, 470, 489.
Linné, C. v., cited, 459, 466.
Llandeilo flags, graptolite fauna, 581, 739, *following* p.503.
Llanvirn beds, Wales, graptolite fauna, 675, 683, 720, *following* p.503.
Lleyn peninsula, Wales, graptolite fauna, 669, 673.
Loch Ryan, slates of, 470.
Logan, cited, 470.
Loganograptus, 508, 537, 544, 554, 563, 568, 571, 573, **630–31**, 637, 744, 745.
kjerulfi, 635.
logani, 504–5, 556, 573, 589, **631–33**, 744, 745.
explanation of plate, 764.
figure, 632.
*mut.* pertenuis, 633.
Lorraine fauna, 490, *following* p.503.
Lossen, cited, 474.
Lower Siluric graptolites, 467, 472, 660, 729.
Lyddeker, cited, 738.

**McCoy**, F., cited, 460, 461, 462, 470, 471, 495, 620, 621, 623, 633, 636, 647, 651, 666, 670, 695, 710, 718.
Malaise, C., cited, 463, 495, 636, 637, 710.
Maquoketa shales, *following* p.503.
Marr, J. E., cited, 463, 464, 471, 478, 489, 554, 555, 567, 640, 736; investigations, 553; mentioned, 567.
Mather, W. W., cited, 459.
Matthew, G. F., cited, 464, 465, 472, 481, 492, 495, 592, 594, 596, 598, 602, 603, 605, 606, 613, 615, 616, 633, 672, 675, 734, *following* p.503; mentioned, 646.
Mechanicville, graptolite fauna, *following* p. 503.
Middle Skiddaw slates, 653.
Mississippi valley, upper Maquoketa shales, *following* p.503.
Moberg, J. C., cited, 463, 464, 599, 695.
Moffat shales, 512, *following* p.503.
Mohawk valley, graptolite from, 585.
Monoclimacis, 546.
Mono-Diprionidae, 544.
Monograptidae, 489, 538, 544, 545.
Monograptidi, 546, 547.
Monograptus, 475, 478, 480, 509, 540, 553.
  pala, 514.
  priodon, 540.
Monopodial branching, 485.
Monoprionidae, 475, 484, 544, 545.
Mossebo, graptolite fauna, 687.
Mt Moreno, graptolite fauna, 498, 499, 508, 550, 589, 626, 627, 646, 664, 665, 678, 680, 685, 687, 689, 699, 713, 715, 717, 719, 720, 722, 725, 728, 730, 734, *following* p.503.
Multiramous forms, 484.
Murchison, R. J., cited, 459, 467.
Nelson, New Zealand, graptolite fauna, 746.
Nema, 487.
Nemacaulus, 487.
Nemagrapsus, 467, 716.
  capillaris, 716, 717.
  elegans, 716.
Nemagraptidae, 544.
Nemagraptus, 544, 571, 717.
Neumayr, cited, 575, 577.
Nevada, graptolite fauna, 498, 505, 507, 690, 715, 738, *following* p.503; Caryocaris from, 737.
New Brunswick, graptolite fauna, 633, 672.
New Zealand, graptolite fauna, 695, 746.
Newfoundland, Tetragraptus zone, 495; graptolite fauna, 505, 507, 589, *following* p.503. *See also* Cowhead.
Niagara group, Dictyonemas in, 509.
Nicholson, H. A., cited, 460–61, 462, 463, 470, 474, 477, 478, 488, 489, 509, 521, 544, 554, 555, 567, 570, 574, 592, 593, 617, 618, 633, 634, 657, 696, 697, 726, 727, 729, 731, 735, 738, 739; investigations, 553; mentioned, 567.
Nilsson, cited, 459, 467.
Normanskill shale, 470, 717, *following* p.503; fauna, 490, 739; Diplograptus in, 468.
Normanskill zone, 490.
North America, graptolites, 469, 472.
North Granville, specimens from, 601.
Norway, graptolite fauna, 471, 636, 651, 673. *See also* Krekling.

**Obverse** aspect, 484.
Oeland, Tetragraptus zone, 495; graptolite fauna, 660, 695, 705, 713.

Oesel, Dictyonema zone, 492; graptolite fauna, *following* p.503.
Ohio valley, graptolite fauna, *following* p.503; upper Maquoketa shales, *following* p.503.
Orleans island, graptolite fauna, 589, 651.
Orthoceras limestone, 495, 498, 660.
Orthoceratites, 467.

**Palaeozoicum**, 736.
Paterula, 739.
Pauciramous forms, 484.
Periderm, 486; histology of, 477.
Perisarc, 486.
Perner, J., cited, 459, 464, 471, 477, 480, 498, 540, 541, 660, 691, 692.
Phycograptus, 717.
Phyllograpta *sp.*, 599.
Phyllograptidae, 530, 545, 546, 547, 550, 563, 564, 567, 571, 573–74, 703–18.
Phyllograptini, 546.
Phyllograptus, 476, 480, 494, 497, 499, 508, 509, 530, 537, 545, 546, 547, 571, 573, 636, **703–6**, 743, 746, *following* p.503.
angustifolius, 495, 497, 499, 506–7, 547–48, 555, 563, 564, 573, 705, 706, 708, **711–14**, 715, 744.
explanation of plate, 778.
figures, 704, 713.
anna, 497, 498, 506–7, 563, 564, 573, 651, 654, 669, 670, 678, 683, 703, 706, **714–16**, *following* p.503.
explanation of plate, 777–78.
figures, 715.
zone, 490, 496–98, 505, 507, 651, 656, 678, 690.
*mut.* pygmaeus, 547, 716.
*mut.* ultimus, 715, 778.
Phyllograptus densus, 679.
folium *var.* typus, 708.
ilicifolius, 480, 497, 506–7, 540, 563, 564, 573, 648, 669, 705, **706–8**, 711, 712, 713, 714, 715, 716.
explanation of plate, 777.
figures, 707.
*var.* grandis, 706, 707, 708.
similis, 658, 660.
stella, 693, 695.
typus, 494, 497, 498, 506–7, 563, 564, 573, 580, 586, 608, 653, 654, 706, **708–11**, 720, 744, 745, *following* p.503.
explanation of plate, 778.
zone, 496-98, 691, 713.
Phyllograptus shale, 505, 507, 651, 660, 670, 673, 676, 681, 691.
Phyllograptus zone, 720.
Phyllo-Tetragraptus beds, 669, 679.
Phylogeny of the graptolites, 478; of orders of graptolites, 548–53; of genera and species of graptolites, 553–67; of Dichograptidae, 553, 554.
Plates, explanation of, 747–83.
Pleurograptus, 537, 544, 566, 571, 701.
linearis, *following* p.503.
Plumularia, 467, 468, 588.
Plumularidae, 474, 521, 575, 577.
Pneumatocyst, 488.
Pneumatophor, 518, 519.
Point Levis, graptolite fauna, 467, 491, 503, 505, 507, 580, 581, 583, 587, 588, 589, 590, 606, 609, 611, 622, 623, 632, 633, 636, 646, 656, 659, 669, 672, 675, 689, 690, 710, 713, 715, 721, 728, 729, 731, 734, 738, 739, 740, 741, 742, 745; Caryocaris from, 737.
Point Levis zone, 495, 651, 656, 660, 675, 710, 720, *following* p.503.

Polish graptolite horizons, 511.
Polypariet, 483.
Polypary, 483, 484.
Polypidom, 483.
Polypier, 483.
Portlock, J. E., cited, 459, 467, 574.
Potsdam sandstone, 493.
Primary disk, 487.
Pritchard, G. B., cited, 743.
Pterograptus, 537, 566.
Ptilograptus, 497, 500, 503, 508, 537, 571, 572, **587–88**; phylogenetic relations of genera, 553.
  geinitzianus, 504–5, 572, **590**.
    explanation of plate, 755.
  plumosus, 499, 504–5, 572, **588–89**, 590, 591.
    explanation of plate, 755.
  tenuissimus *sp. nov.*, 504–5, 572, **591**.
    explanation of plate, 754.

**Quebec** group, graptolite fauna, 466, 468, 469, 471, 490, 579, 659, 672, 690, 697, 713, 721, 728, 731, *following* p.503. *See also* Point Levis.
Quenstedt, F. A., cited, 459, 467.

**Radicle**, 484; term, 509.
Ramsey island, Wales, graptolite fauna, 503, 580, 583, 587, 720, 729.
Rensselaer county, graptolite fauna, 492, 601, 606, 615, 618, 646, 657, 749, 751, 752, 753; Clonograptus beds, 496.
Reticulograptus, 599.
Retiograptus, 468, 486, 499, 508, 509, 518, 539, 545, 546, 570, 572, 574, **732–33**.
  eucharis, 545.
  tentaculatus, 499, 506–7, 574, **733–34**.
    explanation of plate, 781.
Retiolites, 476, 480, 509, 518, 540, 545, 547, 550, 551, 732, 733.
  ensiformis, 727, 729.
  geinitzianus, 732.
  venosus, 733.
Retiolitidae, 545, 547.
Retiolitidi, 546.
Retioloidea, 488, 544, 545, 546, 570.
Reverse aspect, 484.
Rhabdinopora flabelliformis, 600.
Rhabdophora, 474, 544, 570.
Rhabdopleura, 474, 575.
Rhabdosomes, 483, 484; walls of, 486.
Rhizopoda, 575.
Richter, R., cited, 461, 462, 471, 473, 477, 509, 539.
Roemer, F., cited, 459, 465, 620.
Rouvilligraptus, 537, 618.
  richardsoni, 498.
Ruedemann, Rudolf, cited, 464, 465, 466, 471, 472, 478, 480, 487, 490, 492, 542, 601.
Russia, graptolite fauna, 602, *following* p.503.

**St Anne** beds, 715.
St Anne zone, 497, 498, 690, *following* p.503.
St Davids, Wales, graptolite fauna, 505, 507, 585, 610, 646, 669, 673, 675, 683, 693, 695, 739.
St Germain-sur-Ile, graptolite fauna, *following* p.503.
St John (N. B.), graptolite fauna, 472, 492, 495, 505, 507, 594, 596, 597, 605, 646, 672, *following* p.503.
St Lawrence region, graptolite fauna, 740.
Salter, J. W., cited, 460, 470, 634, 636, 657, 660, 735, 736.

Sandhurst, Victoria, Australia, graptolite fauna, 621.
Sargassum, 512.
Sart-Bernard, graptolite fauna, *following* p.503.
Saxony, graptolites, 470.
Scandinavia, graptolite fauna, 470, 492, 633, 657, 673; graptolite zones, correlation table *following* p.503.
Scania, Sweden, graptolite zones, 470, 488, 498; graptolite fauna, 505, 507, 602, 660, 669, 676, 687, 691, 695, 710, 713, *following* p.503; Tetragraptus zone, 647.
Schaghticoke, graptolite fauna, 492, 595, 596, 597, 601, 602, 605, 615, 616, 617, 749, 751, *following* p.503.
Schale, 486.
Scharenberg, W., cited, 460, 473, 475, 476, 509.
Schizograptus, 537, 618.
Schlothheim, E. F., cited, 459, 467.
Schuchert, Charles, acknowledgments to, 458; cited, 493, 503.
Schultze's maceration medium, 481.
Scotland, graptolite fauna, 469, 470, 474, 498, 505, 507, 647, 651, 657, 660, 715, 739, *following* p.503; Tetragraptus zone, 495. *See also* Ballantrae.
Seaweeds, attachment to, 513.
Sedgwick, A., cited, 459, 470.
Sertularia, 467, 468, 477.
Shropshire, graptolite fauna, 474, 669, 673, 675, 683, 691; Caradoc shales, *following* p.503.
Sicula, 473, 474, 484; term, 509; details of structure, 520.
Sicular end of rhabdosome, 484.
Siculaseite, 484.
Sigmagraptus *gen. nov.*, 497, 508, 537, 564, 567, 571, 573, **701–2**.
  praecursor *sp. nov.*, 506–7, 564, 565, 573, 627, 645, **702–3**.
    explanation of plate, 756.
    figure, 702.
Siphonophora, 533, 577.
Skåne, graptolite fauna, 657.
Skiddaw slates, graptolite fauna, 470, 498, 502, 505, 507, 552, 554, 555, 633, 636, 637, 640, 646, 648, 654, 657, 660, 669, 672, 675, 686, 693, 708, 710, 715, 720, 726, 729, 731, 734, 736, 739, *following* p.503. *See also* Ellergill beds.
Sollas, J. W., cited, 464, 540.
South Hartford, specimens from, 601.
Spencer, J. W., cited, 462, 463, 472.
Staurograpsus, 467.
Staurograptus, 508, 549, 573, **612–17**.
  dichotomus, 492, 493, 502, 504–5, 573, 601, 613, **614–17**, 639.
    explanation of plates, 750–51.
    figure, 613.
    *See also* Clonograptus (Staurograptus) dichotomus.
    *var.* apertus *var. nov.*, 561, 566, 573, **617**.
      explanation of plate, 751.
Stipes, 484.
Stock, 483.
Stomatograptus, 476, 518.
Stromatoporidae, 577.
Strophograptus *gen. nov.*, 508, 574, **716–17**.
  trichomanes *sp. nov.*, 506–7, 574, 716, **717–18**.
    explanation of plate, 755.
Suess, cited, 470.

Sweden, graptolite fauna, 488, 489, 490, 636, 651, 710, 720; Tetragraptus zone, 495. *See also* Dalarne; Gothland; Scania.
Synoptic table of distribution of Cambric and Lower Champlainic graptolites of New York, 504–7.
Synoptic table of range of genera of Cambric and Lower Champlainic of New York, 508.
Synrhabdosome, 483. 484.

**Taxonomic** relations of the graptolites, 574–77.
Temnograptidae, 567.
Temnograptus, 508, 537, 566, 567, 568, 572, 573, 617, **618–19.**
  milesi, 617.
  multiplex, 617, 618, 619, 620.
  noveboracensis *sp. nov.,* 506–7, 573, **619–20.**
    explanation of plate, 757.
    figures, 619, 620.
Terminology of graptolites, 482–88.
Test, 486.
Tetragrapsus (bryonoides), 655.
  crucialis, 645.
  quadribrachiatus, 645.
Tetragraptidae, 530, 550.
Tetragraptini, 546.
Tetragraptus, 470, 473, 476, 478, 497, 508, 531, 535, 536, 537, 544, 549, 554, 555, 560, 562, 563, 566, 567, 568, 571, 573, 609, 610, 621, 630, 637, **642–44,** 667, 713, 742, 743, 746, *following* p.503.
  *sp.,* 555.
  acanthonotus, 558, 689.
Tetragraptus amii, 494, 504–5, 536, 552, 573, 643, **647-49,** 657.
    explanation of plate, 768.
    figures, 648.
  approximatus, 608, 666.
  arcuatus, 589.
  bigsbyi, 495, 530, 555, 563, 568, 589, 608, 639, 658, 660, 662, 664, 665, 696, 697, 698.
  bryonoides, 608, 655, 656, 658, 693, 697.
  bryonoides (=serra), 648.
  caduceus, 641, 658.
  clarkei *sp. nov.,* 497, 504–5, 556, 573, 643, **652–53.**
    explanation of plate, 769.
  fruticosus, 494, 504–5, 517, 530, 531, 542, 555, 556, 557, 569, 573, 608, 643, 648, **649–52,** 654, 655, 663, 669, 686, 744.
    explanation of plate, 765, 766.
    figure, 531.
    *mut.,* 652, 653.
    campanulatus, 652.
    tubiformis, 652, 653.
  headi, 556.
  hicksii, 624.
  (Etagraptus) lentus *sp. nov.,* 504–5, 561, 565, 572, 573, 643, 644, **666.**
    explanation of plate, 764.
  pendens, 497, 504–5, 555, 573, 643, **653–55,** 688.
    explanation of plate, 769.
    figure, 654.
  phyllograptoides, 555, 563.
  postlethwaitii, 555.
  projectus, 744.
  pygmaeus *sp. nov.,* 499, 500, 504–5, 565, 573, 643, 661, **664–65,** 686.
    explanation of plate, 771.

Tetragraptus quadribrachiatus, 494, 496, 499, 504–5, 556, 573, 589, 606, 608, 643, 644, **645–47**, 649, 655, 657, 744.
explanation of plate, 768.
figures, 646, 647.
serra, 494, 496, 504–5, 530, 548, 556, 573, 580, 585, 606, 608, 643, 648, 649, **655–57**, 744.
explanation of plate, 768.
figures, 656, 657.
similis, 494, 504–5, 550, 573, 643, **658–62**, 669, 686, 698, 705, 706.
explanation of plate, 770.
figures, 642, 644, 659, 660, 661.
(bigsbyi) similis, 567, 570, 661, 663, 665, 705.
taraxacum *sp. nov.*, 499, 500, 504–5, 530, 531, 560, 561, 573, 643, **663–64**.
explanation of plate, 771.
woodi *sp. nov.*, 573, 643, **662–63**.
explanation of plate, 770.
Tetragraptus beds, 639, 651, 659, 673, *following* p.503.
Tetragraptus zone, 494–96, 501, 504, 506, 508, 540, 636, 646, 647, 648, 660, 664, 665, 669, 670, 672, 675, 687, 710, 746, *following* p.503.
Tetraprionidae, 544, 545, 546.
Thamnograptus anna, 591, 627, 629, 630.
Theca, first, 484, 520.
Thecae, 485; length of, 486.
Thuringia, graptolite shales, 471.
Tornquist, A., cited, 465, 466.
Törnquist, S. L., cited, 460, 462, 463, 464, 465, 470, 476, 480, 483, 484, 489, 495, 536, 550, 551, 599, 636, 651, 660, 669, 676, 678, 679, 680, 681, 687, 695, 696, 704, 710, 734.
Trenton shales, species from, 467, 739, *following* p.503.
Triarthrus becki, *following* p.503.
Tribes Hill, graptolite from, 585.
Trigonograptus, 499, 508, 539, 545, 550, 572, 574, **726–27**, 744.
*sp. ?*, 744.
ensiformis, 499, 506–7, 574, 587, 610, **727–29**.
explanation of plate, 782.
lanceolatus, 726, 727.
Trochograptus, 537, 618.
Troy, graptolite fauna, *following* p.503.
Tullberg, S. A., cited, 462, 463, 470, 488, 489, 495, 498, 592, 651, 657, 660, 678, 679, 687, 704, 710.

Ulrich, cited, 493, 503.
Upper Helderberg group, Dictyonemas in, 509.
Upper Siluric graptolites, 472.
Utica shale, graptolite fauna, 467, 468, 470, 472, 490, *following* p.503; Diplograptus, 510; fragments of seaweeds, 518.
Utica zone, 490.

Vakkerö, specimens from, 605.
van Ingen, Gilbert, acknowledgments to, 458; graptolites photographed by, 481; cited, 594, 601.
Van Schaick island, graptolite fauna, *following* p.503.
Vanuxem, L., cited, 459.
Ventral margin, 486.
Ventral wall, 486.
Vermont, Dictyonema zone, 493; graptolite fauna, 504, 506, 601.

Victoria, Australia, graptolite fauna, 471, 495, 503, 621, 633, 636, 647, 651, 657, 660, 673, 695, 710, 745, *following* p.503; St Anne zone, 498.
Virginia, species from, 467.
Virgula, 487.
Virgularia, 467.

**Wahlenberg**, G., cited, 459, 467.
Walch, cited, 467.
Wales, graptolite shales, 469, 512; graptolite fauna, 471, 490, 503, 505, 507, 579, 581, 585, 588, 602, 636, 648, 657, 691, *following* p.503; Dictyonema zone, 492; Tetragraptus zone, 495. *See also* Llanvirn; Lleyn peninsula; Ramsey island; St Davids.
Walther, Johannes, cited, 465, 478, 511.
Washington county, Dictyonema zone, 493; graptolite fauna, 601, 615.
Waterford, graptolite fauna, *following* p.503.
West Gothland, graptolite fauna, 657, 676.
West Sandlake, graptolite fauna, 606.
Westrogothia, graptolite fauna, 670, 695. *See also* Mossebo.
Whitesand bay, Wales, graptolite fauna, 580, 585, 610.
Whitfield, R. P., acknowledgments to, 458.
Wiman, C., cited, 459, 464, 465, 466, 475, 476, 477, 478, 480, 483, 484, 485, 486, 487, 510, 514, 515, 518, 520, 521, 523, 525, 526, 527, 528, 535, 536, 537, 540, 541, 542, 543, 545, 546, 548, 549, 576, 577, 578, 583, 584, 588, 592, 594, 596, 597, 598, 604, 719; specimens drawn by, 481; graptolites decolored by, 481.
Wood, E. M. R., cited, 459, 465, 471, 484, 525, 536, 550, 631, 633, 634, 637, 638, 640, 641, 643, 644, 648, 667, 673, 675, 676, 687, 690, 695, 696, 699, 708, 709, 713, 717.
Woodward, cited, 735, 736, 737.

Zähne, 485.
Zittel, K., cited, 462, 466, 603.
Zweige, 484.

# GENERAL INDEX

Volume and page numbers are separated by a colon, e.g. 3:199 means volume 3, page 199.


**Abrasives** of New York State, by H. C. Magnus, 1:158–79.
Accessions to collections, 1:206–9.
Adirondack region, field work, 1:7.
Archeology, report on, 1:205.
Attendance at museum, 1:205–6.

**Beauchamp,** William M., Metallic Ornaments of the New York Indians, 2:1–120 (apx. 7); History of the New York Iroquois, 2:125–461 (apx. 7).
Berkshire region, field work, 1:7.
Botany, report on, 1:204–5; 2:1–68 (apx. 6).
Brooklyn quadrangle, remapping, 1:8.

**Cephalopods,** structure of some primitive, by R. Ruedemann, 1:296–341 (apx. 3).
Chazy limestone on Valcour island, Lake Champlain, contributions to the fauna of, by G. H. Hudson, 1:270–95 (apx. 3).
Clarke, John M., Report of the State Paleontologist, 1:1–396 (apx. 3); Percé, a Brief Sketch of its Geology, 1:134–71 (apx. 3); Naples Fauna in Western New York, pt 2, 3:199–454.
——— & Ruedemann, Rudolf, Guelph Fauna in the State of New York, 3:1–195.
Collections, accessions to, 1:206–9.
Culicidae of New York State, 1:241–400 (apx. 5, 2d paging).
Cushing, H. P., Geology of the Vicinity of Little Falls, Herkimer County, 1:1–95 (apx. 1).

**Dutchess** county, Precambrian highlands, 1:195.

**Economic** geology, 1:12–13.
Entomology, report on, 1:202–4, 91-235 (apx. 5, 2d paging).

**Felt,** Ephraim Porter, Grapevine Root Worm, 1:1–55 (apx. 5, 1st paging); 19th Report of State Entomologist, 1:91–235 (apx. 5, 2d paging).
——— & Joutel, L. H., Monograph of the Genus Saperda, 1:1–86 (apx. 5, 2d paging).
Fenno, Frank E., Supplementary List of Plants of Susquehanna Valley, 2:57–60 (apx. 6).

**Geology,** report on, 1:6–197.
Grapevine root worm, by E. P. Felt, 1:1–55 (apx. 5, 1st paging).
Graptolites of New York, pt 1, by Rudolf Ruedemann, 4:457–803.
Guelph fauna in the State of New York, by J. M. Clarke and Rudolf Ruedemann, 3:1–195.
Gypsum industry in New York, by A. L. Parsons, 1:89–157.

**Harlem** quadrangle, remapping, 1:8.
Harrison diorite in the Westchester county area of the Oyster Bay quadrangle, by F. J. H. Merrill and H. C. Magnus, 1:193–94.

Hartnagel, C. A., Notes on the Siluric or Ontaric Section of Eastern New York, 1:342–58 (apx. 3).
Herkimer county, geology of the vicinity of Little Falls, by H. P. Cushing, 1:1–95 (apx. 1).
Highlands, crystalline rocks, 1:6.
Hudson, George H., Contributions to the Fauna of the Chazy Limestone on Valcour Island, Lake Champlain, 1:270–95 (apx. 3).
Hudson schist in the Westchester county area of the Oyster Bay quadrangle, by F. J. H. Merrill and H. C. Magnus, 1:193–94.

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Metallic ornaments of the New York Indians, by W. M. Beauchamp, 2:1–120 (apx. 7).
Mineral resources, statistics relating to, 1:210; St Louis exhibit, 1:210–12.
Mineralogy, 1:13–14; accessions to collection, 1:206–7; list of New York mineral localities, by H. P. Whitlock, 1:1–108 (apx. 2); minerals not commercially important, by H. P. Whitlock, 1:180–92.
Mooers quadrangle, mapping and study, 1:10; surface geology, 1:12.
Mosquitos or Culicidae of New York State, 1:241–400 (apx. 5, 2d paging).

**Naples** fauna in western New York, pt 2, by J. M. Clarke, 3:199–454.
Northeast extremity of the Precambrian highlands, by F. J. H. Merrill, 1:195–97.
Northumberland rock, petrography of, 1:7.

**Ontaric** section of eastern New York, notes on, by C. A. Hartnagel, 1:342–58 (apx. 3).
Orange county, upper Siluric and lower Devonic faunas of Trilobite mountain, by H. W. Shimer, 1:173–269 (apx. 3).
Oyster Bay quadrangle, distribution of Hudson schist and Harrison diorite in the Westchester county area, 1:193–94.

**Paleontology**, report on, 1:198–200; 1–396 (apx. 3).
Parsons, Arthur L., Peat, its Formation, Uses and Occurrence in New York, 1:15–88; Notes on the Gypsum Industry in New York, 1:89–157.
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Pleistocene, 1:8–12.
Precambrian and crystalline rocks, 1:6–8.
Precambrian highlands, northeast extremity, by F. J. H. Merrill, 1:195–97.
Putnam county, crystalline rocks, 1:6; Precambrian highlands, 1:195.

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**St Lawrence** valley, evidences of marine submergence, 1:9.
Salamanca quadrangle, geologic map in cover of v. 1.
Saperda, monograph of genus, by E. P. Felt and L. H. Joutel, 1:1–86 (apx. 5, 2d paging).
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**Westchester** county area of the Oyster Bay quadrangle, distribution of Hudson schist and Harrison diorite, 1:193–94.
Whitlock, H. P., List of New York Mineral Localities, 1:1–108 (apx. 2); Minerals not Commercially Important, 1: 180–92.

**Zoology**, report on, 1:200–2; accessions to collection, 1:207–9.

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